

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

**Are distinct particle spectra an indication of the state of the  
phytoplankton community in St Helena Bay?**

**Murray Crichton**

**Minor dissertation submitted in partial fulfilment of  
MSc (Applied Marine Science)  
In the Department of Zoology  
University of Cape Town  
May 2012**

**Supervisors: Profs. Larry Hutchings and Astrid Jarre**



**UCT  
MARINE RESEARCH  
INSTITUTE**

I know the meaning of Plagiarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own.

(signed electronically)

---

Murray Crichton

University of Cape Town

## Contents

<b>Acknowledgements .....</b>	<b>5</b>
<b>Abstract .....</b>	<b>6</b>
<b>Introduction .....</b>	<b>7</b>
<b>Chapter 1: Literature review .....</b>	<b>11</b>
The size structure of pelagic ecosystems .....	11
Biomass size spectra .....	12
Quantitative analysis of biomass size spectra .....	15
Applications of particle size distributions .....	18
The Coulter Counter .....	19
Phytoplankton population size structure .....	20
Phytoplankton, zooplankton and the pelagic fish .....	24
Hydrodynamics of the southern Benguela current and St. Helena Bay .....	25
Phytoplankton dynamics of the southern Benguela current .....	26
<b>Chapter 2: Research findings .....</b>	<b>33</b>
Introduction .....	33
Methods .....	36
Study site and procedures of the monitoring line .....	36
Sampling procedures .....	38
Wind stress .....	38
Particle size data .....	39
Results .....	43
Upwelling events .....	43
Chlorophyll <i>a</i> and total particle volume .....	46
Particle size data .....	46
Chlorophyll <i>a</i> maximum particle spectra .....	46
Surface particle spectra .....	46
Expected size distribution .....	61
Discussion .....	64
Particle spectra observations .....	65
Food web structure and function .....	68
<b>Chapter 3: Concluding remarks .....</b>	<b>71</b>
Critique of methods .....	71
Wind data, cumulative divergence and defining upwelling .....	71

Particle spectra analyses .....	72
Future work .....	73
<b>References .....</b>	<b>74</b>
<b>Appendix A.....</b>	<b>89</b>
Wind data and cumulative divergence.....	89
<b>Appendix B.....</b>	<b>90</b>
Temperature profiles .....	90
<b>Appendix C.....</b>	<b>90</b>
Particle size spectra .....	90
<b>Appendix D.....</b>	<b>90</b>
Expert system trail.....	90

University of Cape Town

## **Acknowledgements**

Many thanks are given to my project supervisors, Profs Larry Hutchings and Astrid Jarre, for their support in knowledge and kindness throughout the year.

Prof Coleen Moloney also provided valuable support in the early stages of the project, thank-you.

I am grateful to Dr. J.J. Agenbag and Mr.Mbongeni S. Tyesi, Directorate: Oceans Research, Chief Directorate: Oceans and Coasts, Department of Environmental Affairs for their assistance in acquiring wind data and in calculation of upwelling indices.

Financial assistance through the Marine Research Institute at UCT is gratefully acknowledged. Funding for this study was obtained from the SA Research Chair Initiative, funded by the Department of Science and Technology and administered by the National Research Foundation.

## Abstract

The potential of phytoplankton particle spectra to be used as the basis for an indicator of the suitability of feeding habitat for fish recruits in the Southern Benguela was investigated. Phytoplankton samples collected on regular cruises on the St Helena Bay Monitoring Line (SHBML) off Elands Bay on the west coast of South Africa had been analysed with the Coulter Counter and formed the basis of this study. Chlorophyll *a* content of phytoplankton samples was also measured on monthly cruises and with total particle concentration (determined by the Coulter Counter) showed that overall phytoplankton cells represented a significant portion (76%) of samples collected. Surface particle spectra were constructed for the 12 stations on the SHBML for each of 15 monthly cruises between September 2000 and February 2007. QuikSCAT wind data were converted into a cumulative upwelling index and described the seasonality and intermittent nature of upwelling in St Helena Bay. Temperature profiles made from monthly cruise CTD data were used to describe the dynamics of the upper mixed layer. An expert system was constructed, based on theoretical considerations of phytoplankton cell size and growth rate, and used upwelling index and temperature profile information from each cruise to help make consistent decisions regarding the size distribution of phytoplankton cells that should be expected to dominate either the inner bay, frontal area or offshore region at any given time. Observed particle spectra conformed to the expected size distribution, on the whole of the SHBML, on a third of the monitoring surveys, although a 78% success rate was obtained on a per station basis. Deviations from the expected size distribution occurred in all summer months and four of nine winter months. Particle spectra collected from the inner bay during winter months would have the greatest potential as the basis of an ecosystem indicator; the observed size distribution conformed to the expected size distribution 89% of the time. Particle spectra from the frontal area indicated the theoretical state of the phytoplankton community 67% of the time. Small cells ( $< 10 \mu\text{m}$  ESD) were more prevalent than expected in the inner bay, likely due to variability in seeding processes. In the frontal area, cells were also smaller than expected during sustained upwelling and in well-mixed waters, possibly due to advection from further south of unmeasured buoyancy effects. Small cells dominated offshore stations, as expected. The overall interpretation of results was insensitive to the manner of calculating the upwelling index, calculated either as continuous positive divergence or positive divergence without a drop of  $5 \text{ m.s}^{-1}$  wind speed per day. Use of particle spectra as the basis for an ecosystem indicator is limited to the inner bay in winter, the period when fish recruits appear in the bay. In this case, the link between phytoplankton, zooplankton and fish abundance warrants future attention.

## Introduction

Sustainable exploitation and management of fish resources is essential to maintaining current structure and function of marine ecosystems. The implementation of an approach to fisheries management that addresses the social, economic and biological needs is regarded as the way forward (FAO, 2004). Such implementation requires understanding and incorporation of the inherent biological variability of natural ecosystems (FAO, 2003; 2005). The Pelagic system is strongly size dependent and the variability of pelagic fish stocks is linked to variability in size distribution of phytoplankton populations (Fenchel, 1988; Pitcher et al., 1991).

Body size is related to individual life history traits such as growth rate, metabolism, life span and reproductive strategy (Peters, 1983; Brown et al., 2004). These size-dependent processes scale up to the ecosystem level and mediate the trophic interactions and biogeochemical pathways of the pelagic system (Peters, 1983). The microbial food web dominates pelagic systems in oceanic waters when very small cells dominate the base of the food chain whereas a greater proportion of primary production is channelled to larger organisms when phytoplankton communities are dominated by large cells (Fenchel, 1988). The size distribution of phytoplankton components influences the food available to size selective predators, thus influencing food chain dynamics and pelagic fisheries (Pitcher et al., 1991). Marine biogeochemical flows, such as carbon export, are mediated by trophic pathways. The export of carbon production to greater depths, which is responsible for sequestration of atmospheric carbon to marine sediments, is dominated by large-celled plankton (Eppeley & Peterson, 1979; Tremblay et al., 1997; Falkowski et al., 2000; Laws et al., 2000; Brown & Landry, 2001; Le Borgne et al., 2002).

The paradigm mentioned above has led to a large body of research describing the size structure of phytoplankton communities. The most common means of doing so is to construct phytoplankton particle spectra by arranging the size of an organism, irrespective of individual identity, in relation to the abundance, biomass, diversity or production of that size class (Marquet et al., 2005). Various biomass models have been applied to phytoplankton size data which postulate that the abundance in logarithmically equal size classes is constant or decreasing in steady state systems such as the deep open ocean (Sheldon et al., 1972; Platt & Denman, 1977). Regularities in biomass spectra from offshore systems have been observed and patterns of coastal pelagic systems are less regular, but biomass is not randomly distributed (Marquet et al., 2005). Deviations observed for coastal inshore waters, shallow waters, lagoons, estuaries and freshwater lakes have allowed comparative investigations of plankton dynamics among aquatic ecosystems (Gaedke, 1992a).



Size spectra have also been applied to practical considerations such as estimating fish production and growth rates, quantifying the impacts of fishing on the pelagic ecosystem and monitoring the effects of human perturbation of aquatic systems (Sheldon et al., 1977; Sheldon, 1979, 1984; Borgmann & Whittle, 1983; Moloney & Field, 1985; Cottingham, 1999; Bianchi, 2000; Rice, 2000; Zwanenburg, 2000; Vanaverbeke et al., 2003).

Distinct particle spectra exist for newly upwelled, mature and aged water, as well as for different regions of the ocean; hydrodynamics strongly control the distribution of plankton mostly through species-specific competitive interactions of phytoplankton to take up nutrients and remain in the euphotic zone (Margalef, 1978; Legendre & Le Fevre, 1989; Tremblay et al., 1997; Goericke, 1998). The size distribution of phytoplankton cells is controlled by physical conditions (classical bottom-up controls) such as light, water temperature and turbulence, nutrient concentrations and biological interactions (classical top-down controls), such as size selective predation (Margalef, 1978; Alcaraz et al., 1988; Chisholm, 1992; Kiørboe, 1993; Berman & Shteinman, 1998). There is a consistent pattern of large-celled diatoms dominating turbulent, cold, nutrient-rich waters, small-celled mobile flagellates dominating stratified, warm, nutrient-depleted waters and picoplankton present at background levels (Pitcher et al., 1991; Mitchell-Innes & Pitcher, 1992). However, this is a general pattern and the relative importance of top-down and bottom-up controls and their interaction varies from system to system (Fuch & Franks, 2010).

Phytoplankton size spectra have been determined on fresh samples collected on transects off the west coast of South Africa during many cruises because of their usefulness in describing the size structure of plankton populations (Olivieri, 1983; 1985; Olivieri et al., 1985; Armstrong et al., 1987; Pitcher, 1988; Pitcher et al., 1991; Walker & Peterson, 1991; Pitcher et al., 1992). Phytoplankton samples have been collected and analysed for chlorophyll *a* and phytoplankton particle size spectra regularly since April 2000 on a transect off Elands Bay SHBML (Hutchings et al., submitted).

The samples collected by cruises on the SHBML present an opportunity to describe the spatio-temporal distribution of phytoplankton, in a region of high productivity and variability, over a longer time period than has been previously available. Previous studies of phytoplankton within the Southern Benguela have generally been dominated by a taxonomic approach with complementary size-based analyses, discriminating between either large- or small-celled phytoplankton by electronic sizing or chlorophyll *a* fractionation (Walker & Peterson, 1991). Few studies in the Southern Benguela have used particle size spectra to describe phytoplankton dynamics (e.g. Olivieri, 1985;

Olivieri et al., 1985; Armstrong et al., 1987). None have been purely ataxonomic, except the work by Moloney et al. (1991) modelling the size based dynamics of plankton food webs and by Moloney and Field (1985) who used particle size data to predict the potential yield of pelagic fish in the northern and southern Benguela region.

Despite the usefulness of rapid determination and immediate results the Coulter Counter has limitations with respect to analysing phytoplankton samples. The equipment and software is not able to distinguish between living matter and detritus or between autotrophs and heterotrophs (Sheldon et al., 1972; Olivieri et al., 1985;). Cell chains are counted as a single large cell rather than multiple small cells. The Coulter Counter measures displacement volume so that the calculated particle diameter is that of sphere with the same volume as the measured particle (Beckman Coulter, Inc., 2010; [www.beckmancoulter.com](http://www.beckmancoulter.com)). Small particles, in this case less than 2  $\mu\text{m}$  in size, are not counted and larger particles are under-sampled (Vidondo et al., 1997).

The Southern Benguela is the most productive upwelling region in the ocean (Carr, 2001) and supports several fisheries which provide South Africa and many other nations with fish (FAO, 2004). St. Helena Bay is an important pelagic recruitment area within the Southern Benguela. Four to five months after spawning, recruits are abundant in the bay and increase in size as they move southwards through the bay (Crawford, 1980; Hutchings & Nelson, 1985). The semi-enclosed bay receives cold nutrient rich water from cyclonic circulation that originates from an upwelling centre off Cape Columbine, as well as from intermittent coastal upwelling in a narrow band north of St Helena Bay when southerly onshore winds prevail (Armstrong et al., 1987). The dual upwelling plus stratification through sun warming and a high retention time within the Bay allow blooms to develop over 2-10 days and results in a region of elevated productivity (Brown & Hutchings, 1987). Primary productivity estimates for St Helena Bay range between  $0.99 \text{ g C m}^{-2} \text{ d}^{-1}$  to  $7.85 \text{ g C m}^{-2} \text{ d}^{-1}$  whereas average productivity for the Southern Benguela is approximately  $2.0 \text{ g C m}^{-2} \text{ d}^{-1}$  (Brown, 1984; Mitchell-Innes & Walker, 1991).

The variable hydrographic conditions of St. Helena Bay and of the Southern Benguela are responsible for much of the variability of phytoplankton assemblages, the size as well as the biochemical composition (Pitcher, 1988). Winds drive upwelling and are a major control of nutrient availability and therefore phytoplankton dynamics and community structure (Mitchell-Innes & Walker, 1991).

Given the nature of particle spectra data, its limitations and that, in the past, this type of data has been complementary to taxonomic work, are phytoplankton particle size spectra an indication of the state of the phytoplankton community in St. Helena Bay? The aim of this study was to determine the differences between distinct phytoplankton

particle spectra from newly upwelled, mature and aged upwelled water. The current study is exploratory in nature with the outlook to determine whether monthly particle size spectra collected at St Helena Bay may be used to describe food web structure and function on monthly or seasonal scales. Wind and water temperature was used to classify the prevailing hydrographic conditions. Water samples collected at stations on the SHBML from 2000 to 2007 were analysed for chlorophyll *a*, a Coulter Counter Multisizer electronic particle counter was used to enumerate phytoplankton particles and particle spectra were constructed.

University of Cape Town

## Chapter 1: Literature review

### ***The size structure of pelagic ecosystems***

The body size of plankton communities ranges across several orders of magnitude. Conventionally, plankton are classified according to equivalent spherical diameter (ESD) in logarithmic size classes as picoplankton (0.2 – 2µm), Nano plankton (2 – 20µm), microplankton (20 – 200µm) and mesoplankton (> 200µm), and even larger organisms are referred to as nekton (Sieburth, 1979). Prokaryotes are the principal organisms of the picoplankton group although a few eukaryotes fit the size range as well. The nanoplankton comprises photosynthetic forms such as small diatoms, chlorophytes and pigmented flagellates and phagotrophic forms such as non-pigmented flagellates and dinoflagellates. Microplankton contains the commonly known photosynthetic diatoms and dinoflagellates as well as phagotrophic ciliates, dinoflagellates and small metazoan zooplankton. Larger metazoan zooplankton, including copepods, cladocera and rotifers exceed the microplankton size class although some of their larval stages do not (Fenchel, 1988).

Consistent scaling laws exist in pelagic communities. Body size determines the rate of individual physiological processes and community level trophic interactions (Jennings, 2005). Body size scales with biological properties including metabolic rate, intrinsic rates of increase, reproductive output, rates of mortality and longevity (Fenchel, 1974; Peters, 1983; Brey, 1990; Denney, 2002). Aquatic food chains are also size based. Predator prey size ratios are fixed within limits (Fenchel, 1988). Feeding mode restrictions limit the minimum and maximum size of prey a predator may catch such that very small prey items are inefficient to capture and predators are larger than their prey (Sheldon et al., 1972; Dickie et al., 1987; Fenchel, 1988). Observed regularities are evident for the size structure of offshore and freshwater lake ecosystems (Sheldon et al., 1972; Beers & Reid, 1982; Sprules et al., 1983; 1991; Platt et al., 1984; Sprules & Knoechel, 1984; Rodriguez & Mullin, 1986b; Sprules & Munawar, 1986; Echevarría et al., 1990; Ahrens & Peters, 1991; Gaedke, 1993; Quiñones, 1994). The above assumptions regarding pelagic food chains are only valid for steady state systems, which excludes coastal regions (Fenchel, 1988).

Nevertheless, an ataxonomic size based approach can be adopted to study the structure and function of pelagic ecosystems (Platt, 1985; Quinones, 1994; Rodriguez, 1994). Organisms can feed at different trophic levels but, generally, the trophic position increases with mean species body size (Fry & Quinones, 1994; Jennings et al., 2002). It has also been suggested that size is a better descriptor of trophic position than taxonomic identity because the size of an organism over its lifetime may change in

orders of magnitude and where a food web is strongly size structured an organism may start off as a prey item and grow to become the predator (Jennings, 2005).

### ***Biomass size spectra***

The most common representation of size distribution in aquatic systems has been size spectra which relate the size of individuals in a community to the number (or biomass) of individuals in that size class regardless of individual identity (Marquet et al., 2005; White et al., 2007). The aggregation of organisms according to size was proposed as an alternative to taxonomic studies which, at the time were described as difficult. There was also a need for a rapid, repetitive measure of ecosystem structure (Platt et al., 1981).

Particles had been grouped by size before, microscopically (Riley 1963), by filtration (Mullin, 1965) and by light scattering techniques (Jerlov, 1961 cited in Platt et al., 1981). However, electronic particle counting allowed efficient enumeration of ocean particles less than 100  $\mu\text{m}$  in size to yield particle size distributions of the ocean (Sheldon and Parsons, 1967). The Coulter Counter increased the speed and accuracy of particle counting and allowed many particle size distributions of sea water to be constructed with similar accuracy to microscopic determination (Sheldon et al., 1972; Platt et al., 1981; Olivieri, 1985).

Particle count data presented as a frequency distribution of particle ESD (equivalent spherical diameter) displayed a peak of small particles and exponentially fewer counts of larger particles (Sheldon et al., 1972). However, a plot of particle concentration (by volume) versus particle diameter indicated that even though the larger particles were numerically less important they may dominate volume. A diatom bloom at 40  $\mu\text{m}$  only became apparent to Sheldon and Parsons (1967) after plotting their data in this manner. Concentration by volume was calculated by multiplying the numbers by individual particle volumes, giving total volume of particles in the size class, normalised by the total volume of water examined. Particle size diameter was typically presented on a  $\log_2$  scale (Platt et al., 1981). Presentation in this manner was informative and became the standard way of representing particle size data, known as the size or biomass spectrum (Silvert & Platt, 1978; Platt et al., 1981).

Normalisation of biomass spectra was proposed by Platt and Denman (1977) to allow comparison of size spectra with differential logarithmic size class widths. Normalised biomass-size spectra scale the biomass in each size class to the width of that class (Platt & Denman, 1977; Sprules & Munawar, 1986). The approach has been adopted as

the model of choice for many plankton size structure studies (Ahrens & Peters, 1991; Rojo & Rodriguez, 1994).

Sheldon et al. (1972) observed distinct particle spectra for surface waters of polar, temperate, subtropical and equatorial regions. For subtropical surface waters and water at depth at all latitudes a uniform particle concentration over the all size classes was observed (Sheldon et al., 1972). Based on these original observations of biomass spectra for the North and South Atlantic and South Pacific waters Sheldon et al. (1972) postulated that for aquatic ecosystems the number of individuals in logarithmically equal size classes was equal, i.e. a zero slope on a line fitted to the spectrum data (the 'linear biomass hypothesis', Sheldon et al., 1972; Gaedke, 1992a).

Sheldon's (1967) original work was limited to small particles (including a detrital component) and extrapolation to larger particles showed a downward trend (Platt et al., 1981; Gaedke, 1992a). The theoretical basis for Sheldon's hypothesis is based on the trophic level concept. Energy flows between discrete trophic levels. The theory originates from size-dependent nature of the marine food chain (Kerr, 1974). In pelagic ecosystems predators are larger than their prey because of feeding mode restrictions. Filter feeders are restricted by the size of the filtering apparatus and predatory fish restricted by their mouth size (Poulet, 1973; 1977; Boyd, 1976; Azam et al., 1983). It was suggested that these predator: prey size ratios result in the ocean containing more small particles than large particles and equal biomass across each size class of the size spectrum (Elton, 1927; Odum, 1971). Sheldon's model applies to open ocean ecosystems that are theoretically steady state systems (Gaedke, 1992; Quiñones et al., 2003).

Platt and Denman (1977) proposed an alternative analysis of energy flow up the food chain to account for the decline of volume concentration. Their model stated that pelagic food webs are a continuous size spectrum of organisms and that there is a slight decrease of biomass with organism size, providing for an allometric structure for the pelagic ecosystem (Platt and Denman, 1978; Quiñones et al., 2003). Theoretical models of the pelagic community followed (Steele & Frost, 1977; Silvert & Platt, 1978; Kerr, 1979; Vidondo et al., 1997; Rinaldo et al., 2002). A periodic model which fits a quadratic function rather than a linear regression has also been used (e.g. parabolic fitting to trophic levels, Thiebaut & Dickie, 1992; Sprules & Goyke, 1994). Comprehensive biomass spectra show support for the Platt and Denman model (Rodriguez & Mullin, 1986; Quiñones et al., 2003; Marquet et al., 2005).

The allometric relationship of biomass with size does not invalidate Sheldon's flat spectrum hypothesis. The flat spectra, however, may not be constant or equal (Vidondo

et al., 1997). Basic assumptions are made on the energetic basis for uniform distribution of biomass across all size classes (Gaedke et al., 2004). The flow of energy is upward, from small autotrophs to large heterotrophs, i.e. controlled from the bottom-up (Cozar et al., 2003; Gaedke et al., 2004). The assumption is valid for classical food webs, but when the microbial loop dominates, transfer of matter can occur from large to small organisms (Gaedke, 1993). The biomass theories are limited to explaining size spectrum that doesn't include bacteria (Gaedke, 1993). The biomass models also make the assumptions that there is constant growth efficiency throughout the food web and that production rates scale allometrically (Gaedke, 1993; Gamble et al., 2006).

The grouping of particles into discrete size classes results in a loss of data and power in statistical analyses (Vidondo et al., 1997). The discretisation of size classes has also been misinterpreted by the thought that a size spectrum is continuous. Different log bases for the size classes may create size spectra with gaps in the distribution (which there may well be) and results in uncertainty in the estimation of slopes (Vidondo et al., 1997). Normalised biomass size spectra also suffer from uneven weighting of large particles on analyses; often large particles are under-sampled and therefore a single measurement has a disproportionately large influence on the size spectrum (Vidondo et al., 1997).

Modern electronic particle counters are able to examine all particles within a sample making high resolution data on the size axis easy to achieve and with modern computers data reduction is not necessary (Vidondo et al., 1997; Cavender-Bares et al., 2001). Vidondo et al. (1997) suggest that highly resolved size spectra should be presented as probabilities of exceedance (i.e. the probability that any particle taken at random will be larger than a determined size, usually the smallest particle size) and the linear fitting of double log size spectra to a Pareto distribution. The Pareto distribution was first used to analyse income distribution in societies and is a probability density function described by constants of size and scaling which represent the size of the smallest organism and the decrease in probability as size increases (Pareto, 1987 cited in Vidondo et al., 1997). The least-squares and maximum likelihood estimators can be used to estimate the parameters of a Pareto distribution (Johnson et al., 1994; Vidondo et al., 1997). These methods allow determination of parameters that are computed using all observations (particles) and avoids the binning of size data (Vidondo et al., 1997). Gamble et al. (2006) note that the Pareto II distribution is difficult to model and that its parameters are obscure, in relation to ecological events.

### ***Quantitative analysis of biomass size spectra***

Biomass models may not describe all biomass size distributions adequately such as multi-modal distributions and those of highly dynamic systems, yet, they have become an established method for representing size distributions in marine systems. Biomass size spectra have enhanced knowledge on the causes and implications of various plankton population size structures (Marquet et al., 2005; Vidondo et al., 1997).

Normalised biomass-size spectra are most often quantitatively described by three parameters of the straight line fitted to the normalised spectrum (Sprules & Munawar, 1986; Tittel et al., 1998; San-Martin et al., 2006). The parameters are comparable between systems if biomass spectra are constructed in the same manner. The slope indicates the relative number of small organisms to large organisms, the trend of biomass between size classes, and is suggested to indicate the relative productivity of the system (Sprules & Munawar, 1986; Tittel et al., 1998; San-Martin et al., 2006). The y-intercept is an indication of the relative abundance in the system (Sprules & Munawar, 1986). The coefficient of determination gives an indication of the smoothness or continuity of the biomass spectrum and the deviation from the theoretical steady-state (Sprules & Munawar, 1986; Tittel et al., 1998).

The steady-state system originally hypothesised by Sheldon et al. (1972) refers to the size spectrum of a system where abundance or biomass is evenly distributed over logarithmically equal size classes, is the typical size spectrum of an open ocean pelagic ecosystem and is characterised by a straight line with zero slope. If the size spectrum is normalised the equivalent slope is a negative one. A size distribution of a steady state system that has not been logarithmically transformed has the equivalent power law relationship with a size scaling exponent of negative one (Sheldon & Parsons, 1967; Sheldon & Kerr, 1972; Sheldon et al., 1972). Considerable variation in the slope of the line fitted to the normalised biomass size spectrum and the size scaling exponent has been found (Sprules & Munawar, 1986).

Typically, open oceanic waters are characterised by uniform (homogenous) distributions while the particle size distribution of coastal waters, shallow inshore waters and water at higher latitudes is less homogenous (Sheldon et al., 1972; Rodriguez & Mullin, 1986; Witek & Krajewska-Soltys, 1989). Offshore communities characterised by stratified oligotrophic waters exhibit regularities in the biomass spectrum (i.e. are linear) and coastal stations exhibit irregular patterns, for example characterised by dome shaped size distributions (Marquet et al., 2005; Reul, 2006). Deep water lakes were found to have particle size spectra more alike deep ocean spectra than shallow water lakes which were found to have bimodal size distributions (Gaedke, 1992b). Similarly, Sprules and Munawar(1986) reported that open ocean gyres displayed biomass spectra similar



to oligotrophic lakes. Considerable variation in the slope of the line fitted to the size spectra was observed along with irregularities and discontinuities in size spectra (Sprules & Munawar, 1986).

Cavender-Bares et al. (2001) represents size spectra as the probability of exceedance and found that size spectra for different regions (defined by chlorophyll-a, temperature and nutrients) were distinctive, e.g. the North versus South Sargasso Sea and coastal versus jet stream waters. Very little variation in size spectra was observed within each region. Although each region surveyed exhibited different spectra, Cavender-Bares et al. (2001) also found that distinctly different communities yielded very similar size spectra. The difference in slopes of the spectra constructed was not attributed to nutrient levels except at the northern edge of the Gulf Stream where an increase in nutrients resulted in a shallow slope (i.e. an increased dominance of large species).

San-Martin et al. (2006) reported that phytoplankton-normalised biomass size spectra are steep at high latitudes and shallow in equatorial upwelling regions. Slopes are steep at convergent downwelling regions compared to upwelling regions (Piontkovski et al., 2003; San-Martin et al., 2006). Sprules and Munawar (1986) constructed normalised biomass spectra for 32 lakes and ocean gyres and found that the intercept, slope and residual surrounding a straight line fitted to the spectrum were different for the various habitats sampled.

Inter-annual and inter-seasonal variation of biomass-size spectra was studied by Huete-Ortega et al. (2010) off the Iberian peninsula over a longer time period than previous studies. The system studied by the authors was described as dynamic with intermittent upwelling. Phytoplankton abundance and cell size were sampled at different depths at several stations from 1993-2000. Upwelling events in time and space were classified into the stage of the upwelling cycle by using hydrographic parameters that were measured consistently with the collection of phytoplankton samples. Individual size spectra were constructed for each month of the sampling period and were integrated at various levels (e.g. depths, months and stage in upwelling cycle) to elucidate patterns of phytoplankton size structure and test the power law relationship. An inverse relationship existed between cell size and abundance for all size spectra constructed. Depth integrated spectra were representative of the whole water column for a particular station. During upwelling periods a significantly lower negative slope was observed which indicated an increase in the relative importance of larger phytoplankton taxa. Over the entire sampling period a temporal trend towards less negative slopes was observed and attributed to a decrease in abundance of flagellates rather than an increase in abundance of dinoflagellates and diatoms. An inverse pattern was observed in the southern Benguela with flagellates constant and diatoms varying (Mitchell-Innes

&Walker, 1991). The cause for the observed trend in the former study could not however, be determined from the measured environmental variables. Huete-Ortega et al. (2010) concluded that the persistence of the negative power law relationship throughout the study period indicates the importance of bottom up control of phytoplankton size structures. Additionally, deviations from linear regression was not observed even though the system under study was 'dynamic' with intermittent upwelling (Huete-Ortega et al., 2010).

Patterns in regular size spectra exist (examples above) as well as irregular and non-linear size spectra. Biomass distributions that are not linear result from an accumulation of biomass in certain size ranges, creating peaks and bumpy or wavy spectra, or the absence of biomass in size classes, creating gaps and troughs (Gaedke et al., 2004). Irregular size spectra have been dealt with by either flattening the spectra (by integrating over a longer period than environmental fluctuations), attempting to fit nonlinear functions to spectrum irregularities over part of or the entire size spectrum and by using the place and magnitude of irregularities to investigate the underlying mechanisms responsible for the biomass size distribution (Gasol et al., 1991; Gaedke, 1992a, 1992b; Gasol et al., 1997; Cozar et al., 2003; Gaedke et al., 2004).

Gasol et al. (1997) analysed seasonal patterns of size spectra for a freshwater lake based on three years of data. The five peaks in biomass spectrum ESD corresponded to dominant organisms in the lake. Linear and polynomial functions fitted to normalised data were used to test the utility of size spectra in detecting ecological change. The polynomial second order coefficient represented the pattern of prokaryotic dominance; however the slope of the line was not affected.

Cavender-Bares et al. (2001) noted that Gulf Stream waters were characterised by linear size spectra while waters that were not nutrient enriched exhibited 'waviness', with flattening in the  $0.4 \mu\text{m}^3$  ( $\text{ESD} \approx 0 - 9 \mu\text{m}$ ) part of the spectrum. Continental shelf waters were also less linear, but deviated in a different part of the spectrum.

Cózar et al. (2003) hypothesised that irregularity in size spectra are a consequence of ecological interactions, strong top-down effects which act via trophic cascades. Grazing was responsible for irregularities of plankton size spectra in a subtropical lake (Cózar et al., 2003). Alternatively, the flatness of certain size spectra (e.g. steady state systems) reflects the dominance of size-dependent processes which act on the physiological level (Cózar et al., 2003).

Gaedke et al. (2004) hypothesised that biomass distributions that are not linear may be caused by inedible phytoplankton and low weight-specific production rates of small

organisms. The biomass spectra for lakes with pronounced peaks and troughs highlight the role of keystone species. The shape of biomass spectra can be quantified by the existence or absence of size classes with no biomass, the goodness of fit and by looking at the maximum and minimum biomass in each size class. Goodness of fit decreased from more oligotrophic systems to eutrophic systems (Sprules & Munawar, 1986). It was also noted that biomass spectra of higher trophic states are much more irregular than those of lower trophic states such as phytoplankton (Gaedke et al., 2004).

Biomass size spectra, as described above, have been used generally to study the structure of components of the pelagic community (predator prey interactions and energy flow in the trophic system) and as an indicator of ecosystem change. The parameters (slope, intercept and  $r^2$ ) that describe a biomass size spectrum are used in relative terms to compare productivity, abundance and the importance of component size classes.

Beaulieu et al. (1999) used an optical counter to determine size distributions of preserved zooplankton samples. While the main aim of the study was to investigate the utility of the optical plankton counter to accurately enumerate preserved zooplankton samples, the study does provide some insight on analysis of individual size distributions. Classical statistics (t-tests) were applied to histogram count data to detect increase or decrease of size classes with  $\log_2$  bin widths. The authors examined mode shifts of count data that was not binned, between preserved and live samples, but did not describe the quantitative statistics used.

Phytoplankton particle size spectra were constructed by Coetzee et al. (2010) to provide additional information of a pelagic fish survey following the annual northward migration of sardine *Sardinops saga* along the east coast of South Africa. The authors qualitatively describe a plot of interpolated particle size spectra with volume as a function of size along the coast. Although the aim of the study was not focussed on phytoplankton dynamics, the analysis is a brief description of the potential food environment for the sardine, in terms of whether large phytoplankton cells were abundant in an adequate quantity for higher trophic levels. The analysis had no temporal scale.

### ***Applications of particle size distributions***

Besides the application of particle size distributions to furthering understanding of the structure and dynamics of pelagic ecosystems and investigating the spatial-temporal variability among systems, biomass spectra have also been applied to several practical considerations (Schwinghamer, 1981; Sprules & Munawar, 1986; Schartau et al., 2010).

Biomass size spectra were first used to calculate fish production and growth rates (Sheldon et al., 1977; Sheldon, 1979; 1984). Phytoplankton growth could be determined by repeated measurements of particle size and if the standing stock at one size class is known it could be used together with the production to estimate fish production in any other size class (Sheldon et al., 1977). However, the unresolved presence of detritus and curve fitting procedures at the time limited accuracy of results (Sheldon, 1979). Biomass size spectra have continued to be applied to fishery research to estimate and predict the standing stock of pelagic fisheries, fish mortality and fish production (Moloney & Field, 1985; Bianchi, 2000; Rice, 2000; Zwanenburg, 2000).

The targeting of larger individuals by fisheries is reflected in the size distribution of exploited stocks. Size spectra differences between fishing systems exist. The slope and intercept of size spectra of fished populations have been used to detect and quantify the impacts of fishing (Rice & Gislason, 1996; Rice, 2000). The slope is related to the exploitation level and the intercept to system productivity (Bianchi, 2000). Rice and Gislason(1996) found that the slopes of biomass size spectra became steeper and the intercepts decreased for North Sea fish assemblages over time due to the effects of fishing. Comparisons between areas are difficult because of different histories of fishing intensity and the rate of change of size spectra is dependent on the species present and the growth rate of those species (Bianchi, 2000). More recently, the utility of size spectra has been recognised in formulating size-based indicators for the implementation of an Ecosystem Approach to Fishery management (Shin et al., 2005).

Biomass size spectra have been proposed as a tool for monitoring and predicting the effects of anthropogenic nutrient loading in coastal areas (Borgmann & Whittle, 1983; Cottingham, 1999; Vanaverbeke et al., 2003). Biomass spectra may reflect external stress to ecosystems and time series analyses can indicate perturbation from steady state (Sprules & Munawar, 1986). Duarte et al. (2000) quantified the response of phytoplankton communities to anthropogenic nutrient inputs in coastal areas and defined critical nutrient loading levels in a mesocosm nutrient enrichment experiment. The flow of pollutants through food webs has also been analysed with size spectra (Thomann, 1979; 1981; Borgmann & Whittle, 1983; Griesbach & Peters, 1982; Vezina, 1986).

### ***The Coulter Counter***

The Coulter Counter is an electronic particle counter and sizer developed originally for biomedical research. A modified Coulter Counter was used to investigate the nature of particulate matter in the ocean (Sheldon and Parsons, 1966 cited in Sheldon and

Parsons, 1967). The Coulter Counter provides particle counting and size over a size range of 0.4  $\mu\text{m}$  and 1200  $\mu\text{m}$ . Particle solution is aspirated through a 140  $\mu\text{m}$  aperture across which an electrical current flows. The change in electrical impedance between the two electrodes is measured as particles in solution pass through the aperture, and is proportional to the volume of the particle. The number of pulses yields the concentration of particles per unit sample volume. The Coulter Counter calculates equivalent spherical diameter (ESD) and surface area. Equivalent spherical diameter is the diameter of a sphere with the same volume as the particle and surface area is that of a sphere with the same ESD as calculated (Beckman Coulter, Inc., 2010; [www.beckmancoulter.com](http://www.beckmancoulter.com)). The pulse heights which are proportional to particle volume are graded into 128 channels to yield volume per size bins. The size distribution is divided into these size bins. The size of channels varies depending on the number of channels chosen and the effective size range of particles counted, both determined by the operator.

The Coulter Counter has limitations with respect to analysing phytoplankton samples. The equipment and software is not able to distinguish between living matter and detritus or between autotrophs and heterotrophs (Mulligan & Kingsbury, 1968; Sheldon et al., 1972; Olivieri et al., 1985). Cell chains are counted as a single large cell rather than multiple small cells. The Coulter Counter assumes particles are spherical so that the calculated particle diameter is that of sphere with the same volume as the measured particle (Beckman Coulter, Inc., 2010; [www.beckmancoulter.com](http://www.beckmancoulter.com)). Small particles are not counted and larger particles are under sampled (Mulligan & Kingsbury, 1968; Vidondo et al., 1997).

### ***Phytoplankton population size structure***

The use of plankton size spectra (and other techniques) to describe aquatic ecosystems ranging from open ocean to shallow, inshore coastal waters, estuaries, freshwater lakes and lagoons has led to many hypotheses explaining phytoplankton population size structure. Biomass size distributions are shaped by physical, chemical and biological factors and the interaction among these factors. Bottom-up controls, described by physico-chemical variables, are hypothesised to be the more important determinants of phytoplankton size structure than top-down controls, described by biological interactions such as size selective predation and competition interactions. The relative importance of either top-down or bottom-up controls may be dependent on the nutrient state of the ecosystem (Fuchs & Franks, 2010).

The progression in phytoplankton species results primarily from two mechanisms. Succession results from the progression of phytoplankton groups as the characteristics of the water mass changes, e.g. temperature and nutrient concentrations, such that the

phytoplankton groups that dominate have a competitive advantage over other groups under those conditions. Secondly, sequential changes occur when the population of phytoplankton changes due to advection of new phytoplankton into the same area (Pitcher et al., 1991).

### **Physical factors**

Margalef (1978) proposed that the dominance displayed by a particular group of algae was a result of specific adaptations to survive in an environment that varies from turbulent to stable. Turbulence is cited as the most important physical driver of phytoplankton size structure. Turbulence is known to affect phytoplankton populations and the succession of dominant groups because it affects the spectral characteristics of light (important for photosynthesis), the distribution of nutrients and the vertical movement of phytoplankton cells (Berman & Shteinman, 1998). Turbulence influences the persistence of cells in the upper layers of the water body by affecting a cell's dispersion and sinking (Berman & Shteinman, 1998). Berman and Shteinman's (1998) study of turbulence and the dissipation of energy in horizontal and vertical planes from 1992-1996 in the pelagic, epilimnic lake Kinneret in Israel found that dinoflagellate blooms were correlated with periods of exceptionally low turbulence and mixing and when a high input of wind caused turbulent mixing dinoflagellate biomass was low.

Berman and Shteinman (1998) also found that chlorophyll content and primary production were correlated with the dissipation of kinetic energies and vertical mixing. Stronger vertical mixing is likely to increase the influx of nutrients to the euphotic zone and increase the advection of cells from adjacent water bodies causing an increase in phytoplankton biomass in the euphotic zone.

### **Chemical Factors**

The spatial and temporal distribution of nutrients is determined by physical forcing. Nutrient concentration is also an important determinant of cell size. Generally, nutrient-rich water favours the development of large fast growing cells whereas nutrient-depleted water favours the growth of small cells (Kjørboe, 1993). Large phytoplankton favour systems of new production while small phytoplankton have a competitive advantage in systems of regenerated production (Chisholm, 1992). Small cells have a competitive advantage over large cells in a nutrient poor environment because of a high surface area to volume ratio. Surface area affects the maximum nutrient uptake rate and volume dictates the energy requirements of the cell (Margalef, 1978; Fenchel, 1988). Small size is no advantage to nutrient uptake when nutrient concentrations are high (Fenchel, 1988). Motile phytoplankton are able to thrive in nutrient poor waters because they can

swim to patches of nutrients and renew the nutrients around their cell (Kiørboe, 1993; Arin, 2002).

A modelling exercise investigating the effect of size dependent physiological processes on community size spectra showed that on a physiological level energy requirements are responsible for community scale patterns of the power law relationship, which explains the dominance of small and large cells in oligotrophic and eutrophic conditions, respectively (Irwin et al., 2006). The model predictions were most accurate when grazing pressure was low, e.g. in coastal upwelling regions with high nutrient input (Irwin et al., 2006). The model predictions agreed with field observations: an increase in nutrient levels resulted in an increase in biomass at all levels, an increase in large cells relative to small cells and an increase of maximum cell size. There is a minimum nutrient level required for large cells; small cells dominate in nutrient limiting conditions and large cells dominate in nutrient rich conditions (Irwin et al., 2006).

### **Biological interactions**

Zooplankton are thought to have a modulating effect on phytoplankton biomass through grazing and the recycling of nutrients (Alcaraz et al., 1988). Grazing has not been shown to cause termination of phytoplankton blooms because the response by mesozooplankton to phytoplankton blooms is slow (Brussaard et al., 1995). Changes in zooplankton size structure are also unlikely to cause changes in phytoplankton size structure (Havens et al., 1996; Havens, 1998). However, the succession between zooplankton and phytoplankton may be closely linked (Hansson et al., 1998). Grazing directly influences the development and succession of phytoplankton blooms by reducing standing stock and by size selective predation (Brussaard et al., 1995; Hansson et al., 1998). Level of grazing is dependent on turbulence which increases bloom development by increasing nutrient flow, but at the same time reduces bloom development by an indirect effect on copepod grazing (Alcaraz et al., 1988). Alcaraz et al. (1988) found that in a mesocosm experiment copepods graze at a higher rate in turbulent environments.

Fuchs and Franks (2010) modelled phytoplankton and zooplankton as a size spectrum with size dependent nutrient uptake and predation. Ecosystems with larger predator: prey ratios have more efficient transfer of energy between trophic. Plankton predator composition can alter biomass and productivity of lower trophic levels. The authors found that top-down controls can be important in altering the size structure of phytoplankton populations. Size-selective feeding could have a magnitude of effect similar to the addition of nutrients to a system. Predator: prey size ratio and the range of prey size had significant effects on the size structure of the phytoplankton community. Two regimes were modelled. The first regime with specialist predators and large

predator prey: ratios resulted in low omnivory, many top predators and relatively flat size spectra. The second regime with generalist predators and smaller predator: prey size ratios exhibited high omnivory, no top predators and steeper size spectra (Fuchs & Franks, 2010). Fuchs and Franks (2010) concluded that change in the fundamental characteristics of food population can be expected by zooplankton predator community change.

Another interesting finding by the Fuchs and Franks (2010) study is that higher nutrients may result in lower phytoplankton biomass. It occurs when phytoplankton-zooplankton size spectra approach each other at small predator: prey size ratio, and where there are grazers who feed at this border, i.e. on prey their size. The grazers reduce the abundance of large phytoplankton, allow large zooplankton to persist and exert a stronger grazing pressure on phytoplankton (Fuchs & Franks, 2010).

### **Phytoplankton community patterns**

The interaction of multiple physical, chemical and biological controls of phytoplankton size structure is evident from a study by Arin (2002) at an anticyclonic gyre in the Alboran sea in the Mediterranean. Microplankton biomass dominated at the edge of the gyre while pico- and nanoplankton dominated inside the gyre. Picoplankton was more abundant at the surface while nano- and microplankton were more important with depth. Nutrient enrichment explained the dominance of phytoplankton biomass at the edge of the gyre while increased turbulence at the edge of the gyre also contributed to the persistence of large cells in the euphotic zone by decreasing the rate of sedimentation (Arin, 2002). The form of dissolved inorganic nitrate (DIN) could also explain the dominance of either cells larger than 2  $\mu\text{m}$  or smaller than 2  $\mu\text{m}$  cells. At the edge of the gyre DIN was positively correlated with large cell biomass and at the centre of the gyre DIN, in the form of ammonium, was positively correlated to the abundance of small cells (Arin, 2002). The sedimentation or senescence of larger cells from the surface and the input of cells by the advection of adjacent water masses was suggested as the cause for the high abundance of nano- and microplankton compared with picoplankton at the bottom of the mixed layer (Arin, 2002).

In the euphotic zone of upwelling regions there is a predictable succession of phytoplankton from large-celled diatoms to small-celled dinoflagellates. Flagellates and prokaryotes in the picoplankton size range are present at background levels and contribution by larger cells increases as nutrient influxes (Sprules & Munawar, 1986; Ahrens & Peters, 1991; Chisholm, 1992; Arin, 2002; Cullen et al., 2002). The increase in dominance of large cells following nutrient enrichment has also been observed in mesocosm experiments. Duarte et al. (2000) reported an increase in phytoplankton



biomass following nutrient loading that was mostly attributed to an increase in biomass of microplankton. Picoplankton dominated in early days of nutrient enrichment and later on biomass was dominated by microplankton. The relative importance microplankton cells increased as nutrient levels increased.

A seven year study (1993-2000) performed by Huete-Ortega et al. (2010), investigated the inter-seasonal and inter annual variation of phytoplankton abundance in a region with intermittent upwelling located off the Iberian peninsula. The study reported that chlorophyll levels correlated to high phytoplankton abundance, mainly contributed to by large cells. Huete-Ortega et al. (2010) found that at the peak of the upwelling event when upward vertical water velocities are the highest and strong turbulence exists and combined with an offshore wash out of cells the accumulation of large cells is impeded. During the relaxation of upwelling, enhanced nutrient availability, water column stability and reduced dispersion allowed blooms of chain-forming diatoms to establish. Water column stability influences the vertical size structure of phytoplankton communities. Steady state ecosystems, characterised by stratified stable water columns and a permanent deep chlorophyll maximum, are dominated by smaller cells (which have higher light use efficiency than larger cells) at the bottom of the euphotic zone. Whereas, in coastal systems with zero stratified conditions the bottom of the euphotic zone is dominated by large cells. At the end of each upwelling event sedimentation of large fast-sinking cells occurs, i.e. less negative slopes in biomass size spectra are observed. The surface is dominated by smaller cells (Huete-Ortega et al., 2010).

The success of diatoms has been attributed to their inherently fast growth rate, high uptake and assimilation of nitrogen in nitrate rich conditions, high growth efficiency under low light conditions and ability to utilize bicarbonate when CO<sub>2</sub> limits growth of algae (Hobson, 1988; Dugdale & Wilkerson, 1992; Smayda, 1997; Goldman & McGillicuddy, 2003). Also the silica cell wall is resistant to copepod grazing, reticular feeding by small predatory flagellates and pathogens. Diatoms are also able to alter their buoyancy to remain in the euphotic zone (Waite et al., 1992; Smetacek, 1999; Hamm et al., 2003)

### ***Phytoplankton, zooplankton and the pelagic fish***

A large fraction of phytoplankton production flows through the pelagic food chains (Fenchel, 1988). The transfer of energy to higher trophic levels varies with algal species composition. The dominant trophic pathways and transfer efficiency vary with phytoplankton cell size (Cloern & Dufford, 2005). The microbial loop dominates in conditions where very small cells dominate the base of the food chain, as is the case in oligotrophic waters. The import of nutrients favours the dominance of large-celled

phytoplankton communities and under these conditions a greater proportion of primary production is channelled to larger organisms (Fenchel, 1988).

Copepods have a preference for a particular size range of particles and copepod production is not only determined by the total chlorophyll content but also by the particle size (Walker & Peterson, 1991). Copepods are selective feeders and the quality of food available in terms of size, species composition and nutritional state has been linked to copepod fecundity (Morey-Gaines, 1979; Checkley Jr, 1980a; 1980b; Cahoon, 1981; Price et al., 1983; Runge, 1984; Price & Paffenhofer, 1985; Ambler, 1986; Peterson & Bellantoni, 1987; Kiorboe, 1989; Walker & Peterson, 1991; Mitchell-Innes & Pitcher, 1992). Armstrong et al. (1991) reported that the egg production of copepod *Calanoidescarinatus* during the anchor station study in the Southern Benguela was closely linked to phytoplankton food availability which was mediated by hydrological conditions. The authors also noted that phytoplankton cell size, species composition and stage of bloom development increased the understanding of the relationship between food and egg production (Armstrong et al., 1991).

The feeding behaviour of anchovy and sardine is mediated by the size of plankton particles. Sardine and anchovy both filter feed and particulate feed, although the threshold size at which they switch between the two modes is different (van der Lingen et al., 2006). Sardines are principally filter feeders with food particles less than 1200  $\mu\text{m}$  ESD eliciting the filter feeding response. Larger particles are filter-fed at high concentrations but particulate fed at low concentrations. Sardine is highly efficient at filter feeding over the size range 400 to 1200  $\mu\text{m}$  ESD. They are slightly less efficient at retaining particles less than 400  $\mu\text{m}$  ESD but can retain cells down to 10 $\mu\text{m}$  ESD in size, enabling sardines to feed directly on micro-phytoplankton. Clearance increases with particle size and size selectivity for large particles, removed during particulate feeding. Particulate feeding is the primary feeding mode for anchovy. The switch from filter feeding to particulate feeding occurs at particles 700  $\mu\text{m}$  in size (James & Findlay, 1989). The minimum size trapped by Anchovy during filtering is 200 to 250  $\mu\text{m}$  ESD which makes a large portion of phytoplankton unavailable to anchovy. Anchovy select for the largest particles available, generally larger than particles ingested by sardine. The switch in dominance of abundance between small pelagic fish species may therefore be trophodynamically mediated (van der Lingen et al., 2006).

### ***Hydrodynamics of the southern Benguela current and St. Helena Bay***

Upwelling conditions prevail on the entire west coast of South Africa. The southerly winds that drive upwelling are modulated by the east moving cyclones south of Africa, the South Atlantic high pressure system and the pressure field over the continent

(Shannon, 1986). The Southern Benguela is divided from the Northern Benguela by the powerful upwelling cell at Lüderitz at approximately 32°S and to the south extends to the south west coast of South Africa at the approximate position of Cape Agulhas, 20°E (Shannon, 1986). Wind-induced upwelling is strongest during September to April (Shannon, 1986). Additionally, intermittent coastal upwelling circulations prevail along the coast due to local coastal topography and meteorology. The continental shelf is narrow to the South of Cape Columbine and broadens North of Cape Columbine, extending the area of the high biomass coastal waters.

St. Helena Bay is a semi-enclosed bay extending north of Cape Columbine to 32°S. The bay receives cold nutrient rich water from cyclonic circulation that originates from an upwelling centre off Cape Columbine, as well as from intermittent coastal upwelling in a narrow band north of St Helena Bay when southerly onshore winds prevail (Armstrong et al., 1987). The dual upwelling plus stratification through sun warming and a high retention time within the Bay allow blooms to develop over 2 to 10 days and results in a region of elevated productivity (Hutchings et al., 1987). Primary productivity estimates for St. Helena Bay range between 0.99g C m<sup>-2</sup> d<sup>-1</sup> to 7.85 g C m<sup>-2</sup> d<sup>-1</sup> whereas average productivity for the Southern Benguela is approximately 2.0 g C m<sup>-2</sup> d<sup>-1</sup> (Brown, 1984; Mitchell-Innes & Walker, 1991).

### ***Phytoplankton dynamics of the southern Benguela current***

Brown and Hutchings (1985) and Shannon and Pillar (1986) provide a comprehensive review of phytoplankton studies and dynamics in the Southern Benguela current. Early taxonomic studies identified dominant diatom and dinoflagellate species in the Southern Benguela and the contribution of these species to the sardine diet (Boden & Day, 1949; de Jager, 1954). Numerous studies that followed have provided floristic descriptions of the Southern Benguela, at first with none or limited concurrent observation of environmental conditions, but in later studies with increasing cognisance of the environment (Shannon & Pillar, 1986). Shannon and Pillar (1986) mention that the apparent dominance of diatoms reported in early studies might be due to methodological artefacts. Samples were collected by nets and bottles and viewed under low magnification so probably overlooked cells less than 20 µm in size.

Monthly samples collected around the St. Helena Bay region by De Jager (1954) were the first intensive studies of the seasonal change of phytoplankton in the Southern Benguela (Shannon and Pillar, 1986). Month-to-month variability in phytoplankton abundance was observed. Phytoplankton abundance was highest in summer and spring and lowest in winter (De Jager, 1957 cited in Shannon and Pillar, 1986). Cell abundance was higher on the west coast than the south coast of South Africa and

dominated by diatoms. These studies did not account for the pulsed upwelling nature of the Southern Benguela (Brown & Hutchings, 1985). Studies in the 1970s undertook measurements of phytoplankton and chlorophyll during upwelling and downwelling events and found that chlorophyll was not related to cell numbers (Brown & Hutchings, 1985). More intensive sampling followed as the rapidity of the upwelling cycle became apparent and there was interest in the distribution of phytoplankton in relation to upwelling because of its recognised importance in the enhancement of productivity. It was established that newly upwelled water contained low phytoplankton levels, but with the potential to grow because of high nutrient levels. High chlorophyll a levels were recorded in mature upwelled waters (Brown & Hutchings, 1985). A thermal front of phytoplankton biomass with a boundary between low phytoplankton biomass of oceanic water and high biomass in coastal upwelled water was identified. The position of the upwelling front is highly variable, moving with changes in wind direction. The front moves offshore during upwelling periods and onshore during and downwelling periods (Pitcher et al., 1992).

The seasonality of upwelling and concomitant changes of physical, chemical and biological parameters was established by Andrew and Hutchings (1980) and it was suggested that physical factors dominate vertical and horizontal phytoplankton distribution patterns on the west and south west coast (Shannon et al., 1984). Studies reported that phytoplankton biomass was more variable in the summer upwelling season (September-March) than in winter (April to August). A uniform distribution existed in winter due to increased mixing, reduced sunlight and reduced upwelling (Hutchings et al., 1984; Shannon et al., 1984). Phytoplankton concentrations on the south west coast (western Agulhas Bank) relative to the west coast were reported as being moderate because of limited upwelling and strongly stratified waters in summer (Shannon et al., 1984). Seasonal change in the horizontal distribution of phytoplankton was also observed. A higher concentration of phytoplankton was observed in the shallow upper mixed layer because of high light and high nutrient concentrations. The winter biomass was uniformly distributed except where there was persistent upwelling throughout the year (Shannon et al., 1984; Shannon and Pillar, 1986). The composition of phytoplankton species was found to be more diverse in mature upwelled waters and less diverse following upwelling events (Shannon et al., 1984).

The development and decline of phytoplankton populations was monitored. Drogue studies conducted by Hutchings et al. (1983) followed a patch of newly upwelled water and recorded daily measurements of physical, chemical and biological parameters. Previous studies only sampled on a monthly basis (Brown and Hutchings, 1985). The Coulter Counter was first used in the Southern Benguela current in 1984 to construct particle spectra (Hutchings et al., 1984). The study reported that microflagellates are

also numerous in the Southern Benguela. Diatom-chain sized particles dominated the particle volume, microflagellates occurred in background numbers and when bloom-causing diatoms decreased the relative importance of microflagellates increased (Hutchings et al., 1984). Probyn(1985) also reported on the importance of pico- and nanoplankton size class, which accounted for 2-49% and 13-99%, respectively, of the total chlorophyll *a*. These studies highlighted the previously unacknowledged role of the smaller plankton size fractions (Shannon and Pillar, 1985).

The feasibility of estimating phytoplankton size and biomass in fresh and preserved samples from the Benguela current with a Coulter Counter was investigated (Olivieri, 1985). Concurrently, particle spectra obtained from a Coulter Counter were used to describe the growth and decay of three phytoplankton communities (Olivieri et al., 1985). Phytoplankton blooms developed rapidly (Sheldon et al., 1972; Olivieri et al., 1985). Three dimensional spectra were constructed with particle volume, depth and size interval on the axes and were described qualitatively by examining the magnitude, position and timing of peaks in particle volumes. Particle spectra changed during the upwelling cycle; wind reversal caused a change in particle spectra indicating a change in phytoplankton species composition. Water stability (influenced by wind velocity) was reported as important for the sequence of species succession and diversity of the phytoplankton community (Olivieri et al., 1985). It was suggested that changes in the light regime or nutrients may favour particular species. However, the sampling period was brief and the authors indicated that it was unclear whether hydrodynamic forces, nutrient uptake rates or grazing was responsible for determining species composition and cell size (Olivieri et al., 1985). It was noted that the Coulter Counter is not able to distinguish between detritus and living cells, however particle volume was suggested as a suitable indicator of phytoplankton biomass because a significant regression existed between chlorophyll *a* measurements and Coulter Counter particle volume (Olivieri et al., 1985). Taxonomic identification was used concurrently to attribute the peaks to phytoplankton species.

Armstrong et al. (1987) reported on a frontal zone cruise undertaken in December 1984, off Cape Columbine. The fronts were known to affect the distribution of a wide number of organisms including phytoplankton and the position of the upwelling front depended on the prevailing winds. Southerly winds which favour upwelling caused the front to move offshore and winds favourable for downwelling (onshore or quiescent winds) caused the front to move onshore. Armstrong et al. (1987) observed when they analysed phytoplankton particle size spectra across the front, that inshore and frontal phytoplankton communities were different from the offshore population. The pattern observed was consistent with other frontal zones. Phytoplankton biomass was high onshore and decreased at the front, possibly due to mixing and entrainment of oceanic

water at the front. Diatoms dominated at the front and landward of the front whereas smaller nanoplankton cells dominated in oceanic waters. Diatoms preferred well-mixed and transitional water whereas dinoflagellates dominated in stratified water. Diatoms also dominated in surface waters but not deeper where nanoplankton dominated. The hydrographic parameters that were measured simultaneously with the biological parameters were closely linked which highlighted the importance of hydrographic factors in controlling the distribution of phytoplankton populations (Armstrong et al., 1987).

The coupling of the physical regime (driven by wind events), the distribution of nutrients and phytoplankton biomass was again highlighted by a study that sampled stations of spatially variable hydrographic events, transecting recently upwelled, mature and aged upwelled water (Pitcher, 1988). Newly upwelled water on the coast north of St. Helena Bay was characterised by low water temperature, a high concentration of nutrients and low phytoplankton biomass, gradually changing offshore. Similarity analyses indicated two populations, one characteristic of cold, chlorophyll-poor and nutrient-rich water, and the other characteristic of warmer, chlorophyll-rich and nutrient-poor water. Phytoplankton assemblages at stations with similar hydrological conditions were similar and each population was associated with a different stage of upwelling. As the water aged nutrient concentrations (except nitrite) decreased and phytoplankton cell concentration and diversity increased.

A study by Walker and Pitcher (1991) investigated phytoplankton dynamics at stations in St. Helena Bay with similar hydrological properties, in aged upwelled water following the relaxation of an upwelling event and the development of nutrient depleted and stratified warm water. A distinct layered phytoplankton distribution existed within the bay. Large numbers of microflagellates were present at the surface and biomass was dominated by two dinoflagellate species. Phytoplankton biomass at 10 meters depth was dominated by diatoms. A similar pattern was observed in the anchor study mentioned below (Pitcher et al., 1991). The layered phytoplankton structure is representative of a late successional stage of bloom development during a quiescent period after upwelling and before nutrient depletion occurs (Walker and Pitcher, 1991). The study by Walker and Pitcher (1991) and other studies (e.g. Pitcher, 1988) have shown that in the Southern Benguela microflagellates are numerically dominant while diatoms and dinoflagellates dominated biomass and production.

An anchor station study was undertaken at St. Helena Bay for 27 days in March and April 1987 to investigate, amongst other things, phytoplankton dynamics (Chapman and Bailey, 1991). Succession and sequential progression of phytoplankton populations was observed over the three upwelling events that occurred during the sampling period.

Phytoplankton succession took three days and followed the predictable, well known pattern from non-motile small-celled diatoms to larger diatoms, followed by a motile flagellate community. Succession was closely linked to water column stability; initially water was well-mixed and nutrient rich followed by stratified water with a low nutrient availability. The sequential changes in phytoplankton occurred at the end of the second upwelling event and were characterised by a dramatic change in the phytoplankton community composition preceding the advection of a new water mass into the sampling location (Pitcher et al., 1991). Sequential changes of phytoplankton communities in St. Helena Bay are likely to be less frequent than changes of phytoplankton community composition due to succession because St. Helena Bay is less hydrodynamically active than other upwelling regions (Pitcher et al., 1991). The classic succession identified by Pitcher et al. (1991) was accompanied by changes in phytoplankton biomass and production which increased from waters dominated by small diatoms to waters dominated by large diatoms and then declined when the flagellate stage was observed (Mitchell-Innes and Walker, 1991).

The decline in the phytoplankton blooms observed during the anchor station study was preceded by the formation of resting spores and their settling from the euphotic zone. The presence of diatom resting spores and dinoflagellate cysts allowed reseeding of the population when conditions were favourable during the next upwelling cycle. Natural mortality and breakdown of phytoplankton cells in the euphotic zone was the most important mechanism responsible for the decline in phytoplankton biomass. Dispersal and grazing of phytoplankton was minimal (Pitcher et al., 1991). Changes in the phytoplankton species composition was influenced by a combination of variable sinking rates and the level of turbulence, and the competitive advantages of either motile buoyant phytoplankton forms or non-motile forms. Thermal stratification was identified as important for the vertical distribution of the dominant diatom species in the study (Pitcher et al., 1991).

Hydrography and plankton was sampled on a across-shelf transect cruise in 1988 off St. Helena bay, late in the upwelling season during a period of downwelling by Walker and Peterson (1991). Two water types were identified, only partially distinguishable by salinity, but fully distinguishable based on phytoplankton assemblages. The mid-shelf and inner-shelf communities were dominated by diatoms and microflagellates, respectively. The temperature, nutrient concentration, chlorophyll *a* and primary production were similar for both water types, characteristic of aged upwelled water. The fact that only salinity was able to distinguish water type suggests that they were of different origin which also gives an explanation for the different phytoplankton assemblages. The diatom population was seeded from a deep saline layer brought to the surface by strong upwelling. Microflagellate spores originated from less saline water

which would be the single source of phytoplankton when weaker upwelling brings the spores to the surface with simultaneous diatom sinking. However, it was also suggested that the water types may have represented water of different ages and differing stages of succession (Walker and Peterson, 1991). Physical factors, which control seeding and sinking and biological factors, such as grazing, were suggested as important determinants of the phytoplankton assemblage associated with a water mass at a given time (Walker and Peterson, 1991).

Mitchell-Innes et al. (2000) reported that high phytoplankton biomass in the Southern Benguela is predominately due to diatom growth and less so to dinoflagellate growth (Mitchell-Innes et al., 2000). However, other studies have identified flagellates as important contributors to overall growth and production (Barlow et al., 2005). Diatoms seem to associate with cold waters (9 – 13 °C) whereas dinoflagellates (13 – 16 °C) and flagellates (> 14 °C) associate with warmer water (Barlow et al., 2005). This finding confirmed that reported by Mitchell-Innes and Pitcher's (1992) study; a well-defined succession from small to large celled diatoms followed by flagellates was observed as water became warmer, more stratified and nutrient- depleted. An abrupt change in phytoplankton population was recorded when water warmed to 15 °C. Above 15 °C small flagellates with volumes less than 40  $\mu\text{m}^3$  dominated and below 15 °C larger and predominately diatom cells dominated. Subsequently, it was suggested that in the Southern Benguela sea surface temperature (SST) could be used as an index of the age of upwelled water, reflecting the extent of solar warming, stratification, nutrient depletion and their influence on phytoplankton growth (Barlow et al., 2005).

Recent remote sensing studies confirm the patterns of phytoplankton distribution observed by previous ship based studies. Chlorophyll *a* and SST satellite measurements and pigment analyses showed the seasonal cycles of phytoplankton in the Southern Benguela at the class level (Barlow et al., 2005). Phytoplankton biomass (indicated by chlorophyll *a*) is elevated after active upwelling in cool and cold waters. Biomass is high inshore but extended offshore in the summer (Barlow et al., 2005).

Barlow et al. (2006) used remotely sensed SST to indicate the presence of upwelling and performed a pigment analysis of phytoplankton samples. Phytoplankton biomass was calculated from derived indices of pigments for diatoms, dinoflagellates, flagellates and prokaryotes. Inshore communities were dominated by diatoms in cold nutrient-rich water and flagellates dominated warmer water offshore. Dinoflagellates and prokaryotes were present at all stations. Phytoplankton biomass decreased offshore. The inshore-offshore change in phytoplankton population is typical of St. Helena Bay. Flagellates dominate offshore and become more dominant inshore when water is warmer and more



stratified and with intrusions of warm water into the bay. Diatoms dominate below the thermocline (Barlow et al., 2005).

University of Cape Town

## Chapter 2: Research findings

### *Introduction*

The size structure of the phytoplankton community regulates dominant trophic pathways (Cloern & Dufford, 2005). The microbial food web prevails during periods when the phytoplankton community is dominated by small cells whereas the classical food web prevails when the phytoplankton community is dominated by large cells (Fenchel, 1988). The latter state exhibits a higher trophic efficiency, which increases the food available to size-selective predators at higher trophic levels (Fenchel, 1988; Cushing, 1989). The recruitment success of pelagic fisheries is therefore, strongly linked to phytoplankton size structure through the concept of the size-dependent nature of pelagic food webs (Pitcher et al., 1991).

The size structure of phytoplankton communities is partially governed by the relationships between cell size and growth rate. Small cells, which have a high surface area to volume ratio divide rapidly and have a competitive advantage over large cells in nutrient-poor water (Kjørboe, 1993). Surface area affects the maximum nutrient uptake rate and volume dictates the energy requirements of the cell (Margalef, 1978; Fenchel, 1988). Small size is no advantage to nutrient uptake when nutrient concentrations are high so large cells dominate surface waters. Small phytoplankton also have a competitive advantage in systems of regenerated production (Chisholm, 1992), but suffer from increased grazing pressure from small, but more numerous herbivores.

In upwelling regions, wind-driven enrichment of nutrients into the euphotic zone initially favours the growth of rapidly dividing small cells. Slow-growing large cells next dominate surface waters, because their generation time is slower but high nutrient concentrations favour their growth. Upwelled water warms at the surface and stratifies and nutrients are rapidly depleted by the growth of phytoplankton in the euphotic zone. Subsequent nutrient-depletion favours the growth of small, motile forms of phytoplankton (Moloney et al., 1991). During quiescent conditions small cells are present at background levels and following upwelling, as nutrients mix upwards, larger cells become more prevalent. The increased turbulence also contributes to the persistence of large cells in the euphotic zone by decreasing the rate of sedimentation (Kjørboe, 1993; Arin, 2002).

A common tool used in size-based analyses of aquatic food webs is biomass size spectra which relate the size of an individual in a community to the number or biomass of individuals in its size class regardless of individual identity (Silvert & Platt, 1978; Platt et al., 1981). An electronic particle counter and sizer (the Coulter Counter originally used in biomedical research; [www.beckmancoulter.com](http://www.beckmancoulter.com)) allowed the efficient

enumeration of ocean particles less than 100  $\mu\text{m}$  in size and the creation of particle size distributions of ocean water (Sheldon & Parsons, 1967; Sheldon et al., 1972). A plot of particle concentration (by volume) versus particle diameter was the original representation of the biomass or size spectrum. Early observation of distinct particle spectra for surface waters of the North and South Atlantic, as well as the South Pacific and uniform particle concentration at depth in these waters, resulted in R.W. Sheldon postulating a 'linear biomass hypothesis' (Sheldon et al., 1972). Important theoretical considerations regarding the biomass spectrum and trophic energy flow followed (Platt & Denman, 1977; 1978; Silvert & Platt, 1978; Platt et al., 1981; 1984; Kerr & Dickie, 2001). Sheldon's original work considered particles in the phytoplankton size range but work on the topic has been extended to include organisms many orders of magnitude larger in size (Sheldon & Kerr, 1972).

Normalisation of biomass spectra allow comparison of size spectra with differential size class widths and with other modifications this type of biomass spectrum (most often termed normalised biomass size spectra) has become a standard approach for size-based studies of aquatic ecosystems (Platt & Denman, 1977). The parameters of straight lines fitted to spectra are used to describe relative productivity, abundance and other components of the pelagic community (Sprules & Munawar, 1986; Tittel et al., 1998; San-Martin et al., 2006). Biomass spectra have been used to calculate fish production and growth rates (Sheldon et al., 1977; Sheldon, 1979, 1984; Bianchi, 2000; Rice, 2000; Zwanenburg, 2000), in the formulation of size-based indicators of ecosystem change (Shin et al., 2005), and as a tool for monitoring and predicting the response of phytoplankton communities to the effects of anthropogenic nutrient loading in coastal areas (Borgmann & Whittle, 1983; Cottingham, 1999; Vanaverbeke et al., 2003).

The Coulter Counter's first use in the Southern Benguela was to determine the feasibility of estimating phytoplankton size and biomass in fresh and preserved samples (Olivieri, 1983). Subsequently, phytoplankton particle size spectra have been found to show differences between diatom-dominated and flagellate-dominated blooms (Hutchings et al., 1984). Phytoplankton particle spectra also change during the upwelling cycle indicating a change in phytoplankton species composition (Olivieri et al., 1985). Relatively flat spectra exist in oceanic waters and large cells dominate at the upwelling front and landward (Armstrong et al., 1987). Distinct mid-shelf (large-celled) and inner-shelf (small-celled) phytoplankton assemblages exist in aged upwelled water.

Particle size spectra along with taxonomic work have been used to describe plankton dynamics in the Southern Benguela, in the past. The state of the phytoplankton community is strongly coupled with hydrographic conditions (Armstrong et al., 1987;

Pitcher, 1988; Walker and Pitcher, 1991; Pitcher et al., 1991; Mitchell-Innes and Walker, 1991; Walker and Peterson, 1991). Distinct phytoplankton assemblages are associated with a different stage of upwelling (Pitcher, 1988). Phytoplankton particle spectra have also been used to predict potential pelagic fish yields (Moloney & Field, 1985).

Particle spectra have been collected sporadically in the past (since the 1980s) but recently (since 2000) have been collected on regular cruises of the St. Helena Bay Monitoring Line (SHBML) off the West Coast of South Africa (Hutchings et al., submitted). The analysis of samples for phytoplankton particle spectra by the Coulter Counter has been chosen as an efficient method to obtain a snapshot of the phytoplankton community and valuable for monitoring rapid changes that occur following newly upwelled water (Olivieri et al., 1985). Microscopic work requires more time and skill to efficiently analyse samples, and for the most part cannot be done at sea and thus no microscopic taxonomy was undertaken when these samples were collected.

Despite the usefulness of the Coulter Counter it is unable to distinguish between phytoplankton cells and non-phytoplankton cells such as, detritus and autotrophs (Sheldon et al., 1972; Olivieri et al., 1985). The total volumetric displacement of a particle is measured; the software calculates the ESD of the particle from that of a sphere with the same measured volume (Beckman Coulter, Inc., 2010; [www.beckmancoulter.com](http://www.beckmancoulter.com)). Consequently, cell chains are measured as one large cell rather than individual small cells. The size of particles that can be measured is limited, in this case to particles between 2 and 86  $\mu\text{m}$  ESD. Larger particles are under-sampled (Vidondo et al., 1997).

The Southern Benguela is a very productive upwelling region and supports several fisheries which provide South Africa and many other nations with fish (Carr, 2001; FAO, 2004). St. Helena Bay is an important pelagic recruitment area within the Southern Benguela. Four to five months after spawning, recruits are abundant on the west coast and increase in size as they move southwards, passing through the bay (Crawford, 1980; Hutchings & Nelson, 1985). The semi-enclosed bay receives cold nutrient rich water from cyclonic circulation that originates from an upwelling centre off Cape Columbine, as well as from intermittent coastal upwelling in a narrow band north of St. Helena Bay when southerly alongshore winds prevail. The dual upwelling plus stratification through sun warming and a high retention time within the bay allow blooms to develop over two to ten days and results in a region of elevated productivity (Brown & Hutchings, 1987). Primary productivity estimates for St. Helena Bay range between  $0.99 \text{ g C m}^{-2} \text{ d}^{-1}$  to  $7.85 \text{ g C m}^{-2} \text{ d}^{-1}$  whereas average productivity for the Southern Benguela is approximately  $2.0 \text{ g C m}^{-2} \text{ d}^{-1}$  (Brown, 1984; Mitchell-Innes & Walker, 1991).

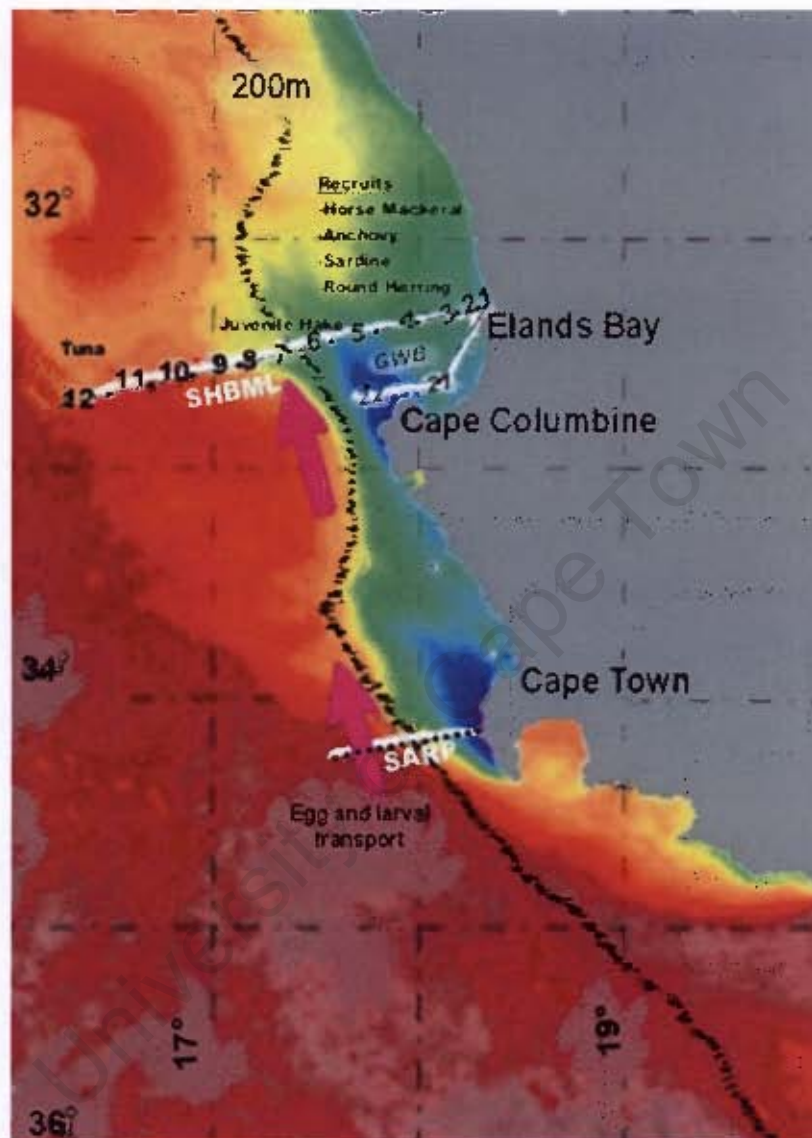
Given the nature of particle spectra data, its limitations and that, in the past, this type of data have been complementary to taxonomic analyses, are phytoplankton particle size spectra an indication of the state of the phytoplankton community in St. Helena Bay? The aims of this study are to determine the differences between distinct phytoplankton particle spectra from newly upwelled, mature and aged upwelled water and to assess the use of particle size spectra to indicate food web structure and function in St. Helena Bay. This project is a first step in establishing the possibility of developing an indicator of the condition of the feeding habitat of recruiting pelagic fish based on particle size data, in combination with zooplankton observations.

## ***Methods***

### **Study site and procedures of the monitoring line**

Full details of the procedures of the monitoring line can be found in Hutchings et al. (submitted). In brief, sampling has been conducted since April 2000 on South African research vessels FRS Africana and FRS Algoa off Elands Bay along the SHBML at

as reduced solar heating and less upwelling reduce the contrast between inshore and offshore water masses.



**Figure 1** Thermal image of the ocean on the west coast of South Africa indicating the upwelling of cold water (blue - green) off Cape Columbine and warm surface water (orange - red) originating from the Agulhas Bank. The position of the 12 stations sampled on St Helena Bay Monitoring Line is also indicated. The 200m isobath is indicated. Taken with permission from Hutchings et al. (submitted).

Data from 15 cruises, over the period from September 2000 to February 2007, were analysed for the study. On occasions, CTD data were unavailable and samples were not collected for one or two stations (Table 1).

**Table 1** Summary of cruises from which data were analysed. The last two columns indicate the stations with samples without CTD or phytoplankton samples

Cruise I.D.	Year	Month	Day	CTD	Particle spectra
ALG083	2000	September	11 - 13		1
ALG088	2000	December	12 - 13		12
ALG089	2001	January	9 - 10	8-12	1
ALG091	2001	February	5 - 7		
ALG094	2001	April	9 - 10		
ALG096	2001	June	4 - 5		12
ALG110	2002	June	21 - 22	1, 2	
ALG118	2002	December	18		
AFR179	2003	June	20 - 21	4-7, 11, 12	11, 12
ALG131	2004	September	28 -29		
AFR202	2004	December	17 - 19	10	10
AFR219	2006	June	27 - 28		12
AFR222	2006	August	2 - 3		
AFR224	2006	August - September	31 - 1	11, 12	
AFR230	2007	February - March	28 - 1		1

### Sampling procedures

The hydrographic characteristics and fluorescence profiles of the sampled stations were determined by CTD casts sampling close to the sea floor and at shallower depths corresponding to the fluorescence maximum, the thermocline and at the surface by a Seabird 9100 CTD. Water samples were collected at the same near surface depths as the CTD and analysed for chlorophyll *a* and phytoplankton. Phytoplankton cell numbers and size were enumerated onshore by a Coulter Counter Multisizer electronic particle counter (Beckman Coulter Inc., model TA II).

### Wind stress

Four times daily NCEP/ NCAR re-analysis wind data (Kistler et al., 2001; downloaded from <ftp://ftp.cdc.noaa.gov/pub/Datasets/ncep.reanalysis/surface>) were extracted for July 2000 to June 2007 at Cape Columbine (32.50°S, 17.50°E) and averaged daily. The coastal orientation (the angle the landward side of the coastline makes with a vector pointing north) was taken as 147° (Pers. Comm. Dr. J.J. Agenbag, Department of Environmental Affairs (DEA): Oceans and Coasts). The principal component of wind stress was taken parallel to the coast, its magnitude taken as,

$$\tau = C_d \rho_a V_y^2$$

Where  $C_d$  is the drag coefficient, which is a function of wind speed (Large and Pond, 1981; Trenberth, 1990),  $\rho_a$  is the density of air (taken as  $1.22521 \text{ kg.m}^{-3}$ ) and  $V_y$  the alongshore wind component in  $\text{m.s}^{-1}$  (Bakun, 1973). The Ekman divergence in  $\text{m}^3.\text{s}^{-1}$  per 100m of coast can be estimated from the wind stress, the density of the upper water layer ( $\rho_w = 1026.17 \text{ kg.m}^{-3}$ ) and the Coriolis parameter ( $f$ ) as (Bakun, 1973),

$$S = \frac{\tau}{\rho_w f}$$

Using the daily divergence values, upwelling events are defined as continuous positive divergence and corresponds to uninterrupted equatorward wind parallel to the coast (Roy et al., 2001). Cumulative divergence for each upwelling event was calculated (see Appendix A for full details of equations). Additionally, as a sensitivity analysis, an investigation of whether the results would be sensitive to an alternative definition of cessation of upwelling (i.e. continuous positive divergence and without a decrease of wind speed of more than  $5 \text{ m.s}^{-1}$  from day to day) was undertaken.

Phytoplankton blooms last six to seven days and events over five to 15 days are important for phytoplankton growth and decay so the focus was on cumulative divergence 20 days prior to sampling (Brown & Hutchings 1987; Mitchell-Innes et al., 2000).

### Particle size data

The Coulter Counter Multisizer, fitted with a  $140\mu\text{m}$  counting aperture, measured particles between 2 and  $86 \mu\text{m}$  ESD and a standard 20ml sample was counted, based on a calibration with known sized particles prior to each cruise. Particle solution is sucked through the aperture across which an electrical current flows. The change in electrical impedance between the two electrodes is measured as particles in solution pass through the aperture, and is proportional to the volume of the particle. The number of pulses yields the concentration of particles per unit sample volume. The Coulter Counter calculates equivalent spherical diameter (ESD) and surface area. Equivalent spherical diameter is the diameter of a sphere with the same volume as the particle and surface area is that of a sphere with the same ESD as calculated (Beckman Coulter, Inc., 2010; [www.beckmancoulter.com](http://www.beckmancoulter.com)). The pulse heights (proportional to particle volume), graded into 128 channels, yields volume per size bins. The size distribution is divided into these size bins. The size of channels varies depending on the number of channels chosen and the effective size range of particles counted, both determined by



the operator. Operators of the Coulter Counter comprised various scientific and technical personnel of the Branch: Ocean and Coasts, DEA.

The size of particles analysed ranged between 4 and 86  $\mu\text{m}$  ESD. At the upper end of the size range too few particles were counted, so for statistical purposes all size bins with counts of less than 10 were excluded from analyses. An anomalous peak of particles less than 4  $\mu\text{m}$  ESD was observed in the particle spectra of samples that were analysed with channels that graded particles less than 4  $\mu\text{m}$  ESD (see appendix C). This occurred because of electrical interference and saturation of these low channels of the particle counter. Consequently, particle channels that counted particles less than 4  $\mu\text{m}$  ESD were excluded from analyses.

The coulter counter software yields the number and concentration of particles per sample. The concentration is in the form of particle volume per sample volume ( $\mu\text{m}^3.\text{ml}^{-1}$ ) and was plotted against particle size class (which represents the graded size channels) to yield the particle spectra, or size distributions, used in all further analyses and presented in 3D format (below). Particle concentration (by volume,  $V$ ) was normalised ( $NV$ ) for the width of the size class ( $d_x - d_{x-1}$ ), by dividing the particle concentration of each size channel by the size width of that channel, before plotting the size distributions:

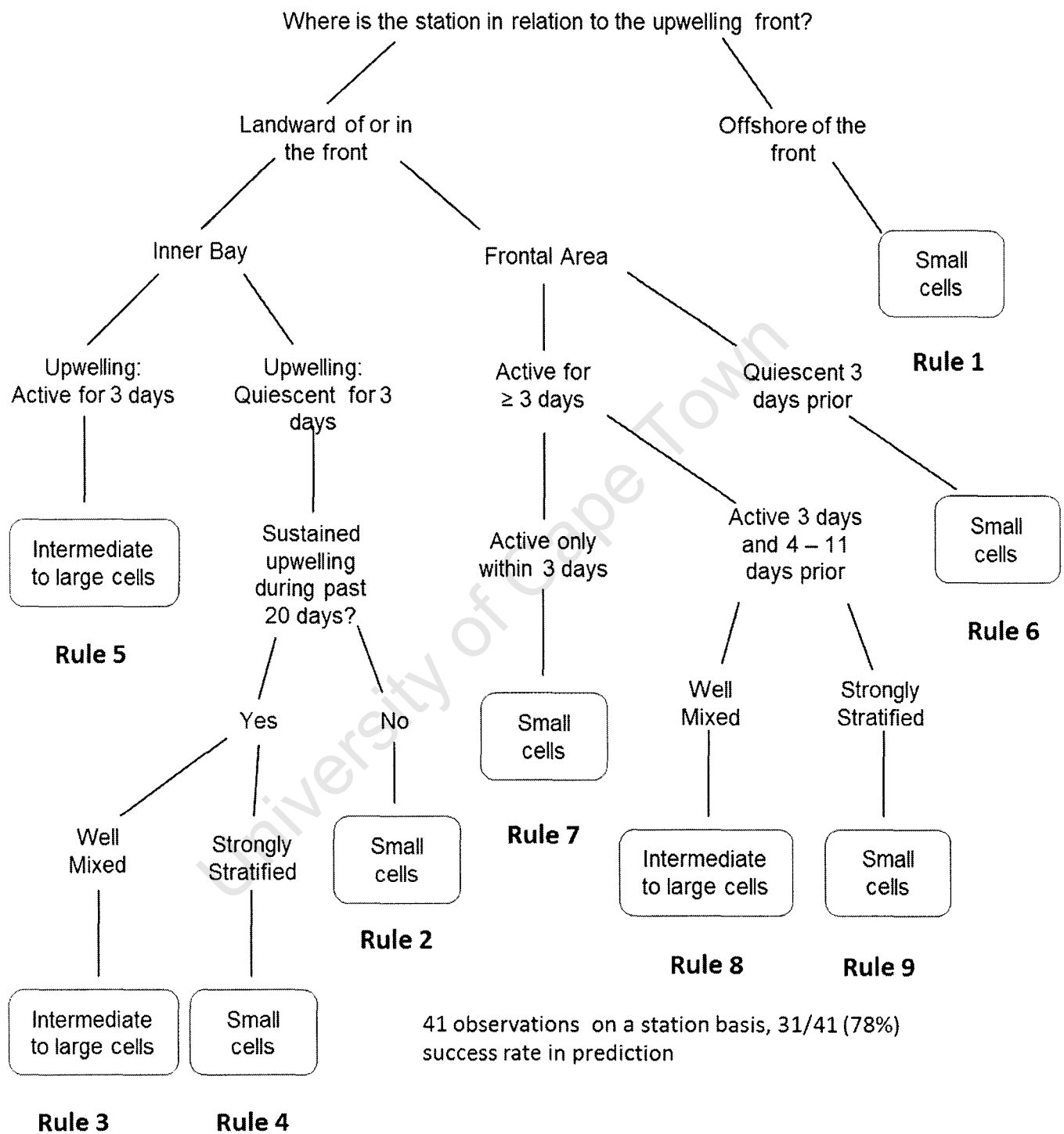
$$NV = \frac{V}{d_x - d_{x-1}}$$

Particle spectra were constructed for surface samples and for chlorophyll *a* maxima. Few obvious subsurface particle maxima were observed. Hence, surface samples were used to typify the phytoplankton community and formed the primary source of information in later analyses. Phytoplankton in inshore and frontal zone waters are generally uniformly distributed in the sun-warmed upper water layer which develops after upwelling. Occasionally, subsurface particle maxima occur offshore and in the frontal zone and represent sinking of the upwelling front (Andrews and Hutchings, 1980) and not the upper mixed layer. Additionally, the hydrographic conditions monitored in this study indicated dynamics of the upper mixed layer.

The total particle concentration (by volume) for each sample was calculated by summing the normalised concentrations of each size bin per sample. The relationship between total particle concentration and chlorophyll *a* was investigated with correlation analyses using *Statistica* (version 10, STATSOFT) for each cruise and using all surface and subsurface samples. Pearson's correlation coefficient was computed for bivariate normal samples and Spearman's rank correlation coefficient was computed for non-bivariate normal samples.

The observed particle spectra were compared with the size distribution of phytoplankton cells that would be expected to dominate a particular water mass at any time. This analysis was done so that the likelihood of phytoplankton particle spectra accurately indicating the state of the phytoplankton community could be assessed and during which hydrographic conditions or locations within St. Helena Bay. The data used for this comparison was the location of the maximum peak in volume of each particle spectra. The likelihood of either small ( $< 10 \mu\text{m}$  ESD) or intermediate ( $10 - 30 \mu\text{m}$  ESD) to large ( $> 30 \mu\text{m}$  ESD) cells dominating particle spectra at stations at the inner bay, frontal area or offshore and taking into account upwelling and the temperature profile was determined. The expected size distribution was based on the theoretical relationship between cell size and growth rate ('size-based theory').

Additionally, a decision tree based on theoretical considerations was designed to ensure the decisions regarding the expected size distribution on individual cruises were consistent (Figure 2). Furthermore, an expert system was built based on the decision tree and as a tool for communication of size-based theory used in this project and of the decisions. Expert systems allow the user to arrive at the same decision as an 'expert' and allow consistent decisions to be made. A strength of expert systems are the explanations provided for each question and decision and enable 'non-experts' to understand the knowledge and logic of the model. Expert systems of this context were originally used in conservation management problems (Starfield & Bleloch, 1983). The expert system was developed using WinExp software and is a series of multiple-choice questions and a set of rules which infers a decision based on answers to the questions (Quadling & Quadling, 1995; Miller & Field, 2001; see Appendix D for outline of the expert system and electronic appendix for the software version).



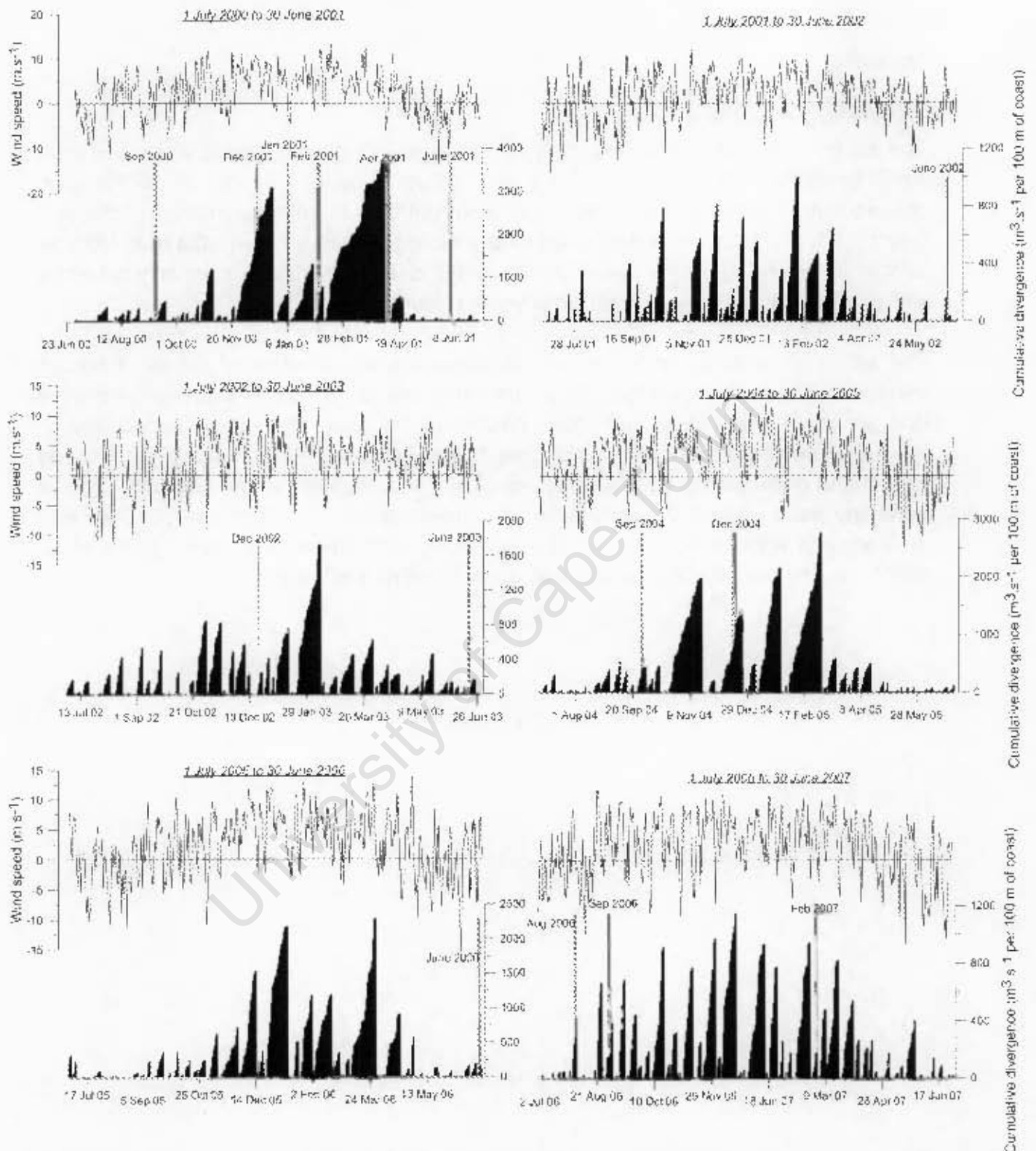
**Figure2:** Decision tree used to determine the dominance of phytoplankton cells either in the inner bay, frontal area or offshore and taking into account upwelling information and temperature profiles. 'Active' or 'Quiescent' refers to the state of upwelling and 'Well-mixed' and 'Stratified' refers to the upper layer of the water column. Decisions are in rounded boxes and the branches are numbered with the corresponding rules in the expert system.

## **Results**

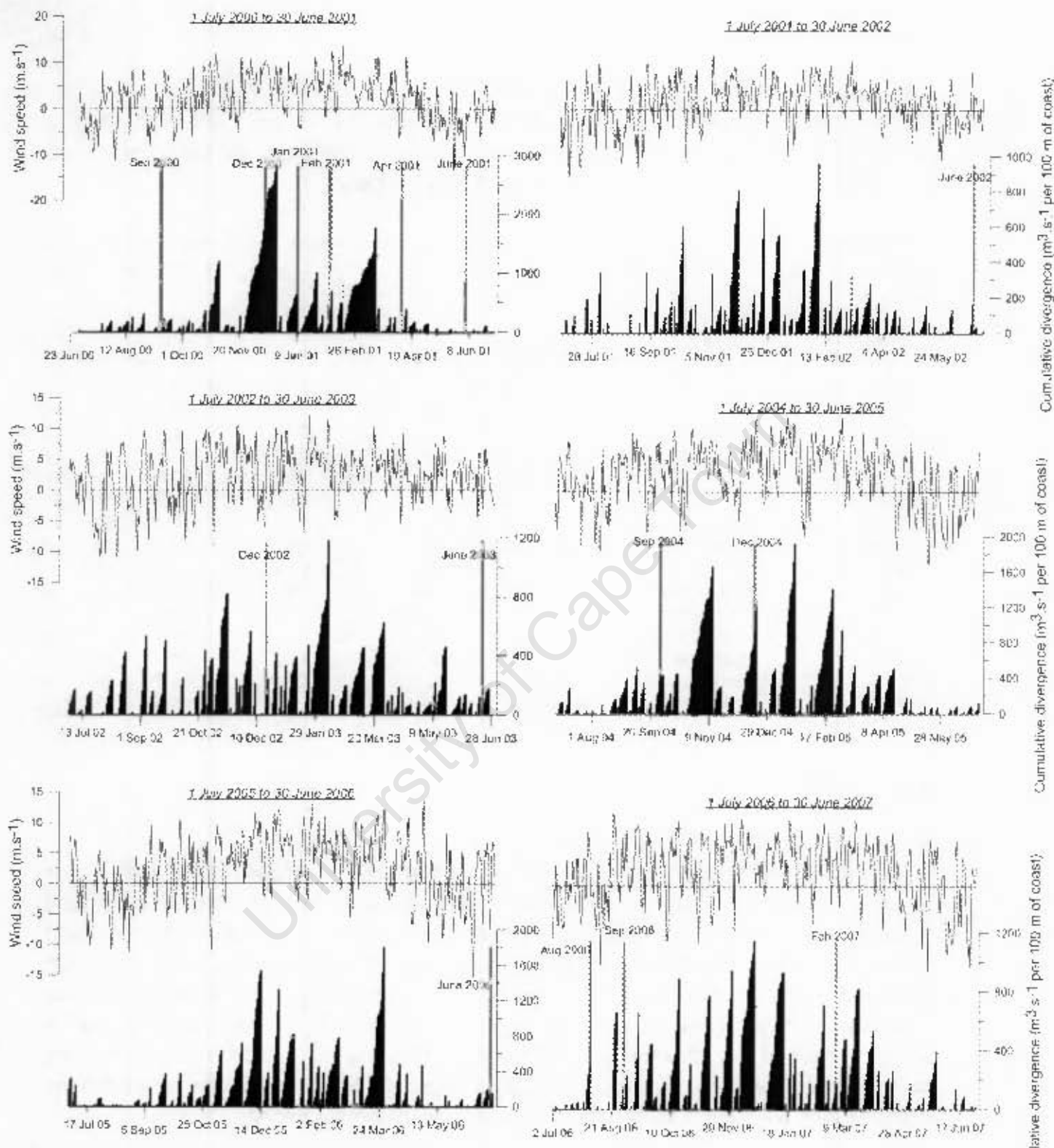
### **Upwelling events**

The seasonality of the upwelling cycle is displayed in Figure 3. Winds weakened from April (justifying classifying April as an autumn/ winter month) to September, consequently upwelling events were less powerful than in summer months (October – March). Wind-induced upwelling events were more frequent and powerful from October to March. Upwelling during period of July 2000 to June 2001 was unusually powerful, with longer upwelling events than other years (Figure3).

The sensitivity analysis revealed that defining upwelling in either of the two methods mentioned above did not affect the overall interpretation of results. Defining cumulative divergence as continuous wind speed parallel to the coast and without a decrease of wind speed of more than  $5 \text{ m.s}^{-1}$  from day to day increased the frequency of upwelling events and decreased the duration of powerful upwelling events. The seasonal cycle of upwelling was maintained (Figure 4). As the choice of a  $5 \text{ m.s}^{-1}$  drop in wind speed was arbitrary and without previous support, upwelling defined as was done by Roy et al. (2001; i.e. any positive divergence) was used in further analyses.



**Figure3:** Daily time series of wind speed parallel to the coast ( $\text{m.s}^{-1}$ ) at Cape Columbine from 1 July 2000 to 30 June 2007 (line graph in each panel) and cumulative divergence ( $\text{m}^3.\text{s}^{-1}$  per 100 m of coast) per upwelling event (bar chart in each panel) for the same time period. Upwelling is positive divergence. Grey bars indicate dates of cruises. The period from 1 July 2003 to 30 June 2004 is not shown because no particle spectra samples were taken within that time. Note scale changes for divergence.



**Figure 4:** Daily time series of wind speed parallel to the coast ( $\text{m.s}^{-1}$ ) at Cape Columbine from 1 July 2000 to 30 June 2007 (line graph in each panel) and cumulative divergence ( $\text{m}^3.\text{s}^{-1}$  per 100 m of coast) per upwelling event (bar chart in each panel) for the same time period. Upwelling was terminated by a drop in wind speed  $5 \text{ m.s}^{-1}$  per day or more. Grey bars indicate dates of cruises. The period from 1 July 2003 to 30 June 2004 is not shown because no particle spectra samples were taken within that time. Note scale changes for divergence.

### Chlorophyll a and total particle volume

The relationship between total particle concentration (by volume) and chlorophyll a accounted for 76% of the variation in the data for all cruises and for individual cruises accounted for a significant portion of the variability (Table 2).

**Table 2** Results of correlation analyses for total particle concentration (by volume;  $\mu\text{m}^3\text{.m}^{-1}$ ) and chlorophyll a ( $\text{mg.m}^{-3}$ ) per cruise and overall, including all depths. Coulter Counter channels with less than ten particles were excluded from analyses.

Cruise	Date	Test, $\alpha = 0.001$	$r^2$	r	t	p	N	df = N-2
All cruises	September 2000 - February 2007	Spearman's rank correlation	0.76			<0.001	680	678
Alg083	September 2000	Pearson's correlation		0.96	18.78	<0.001	35	33
Alg088	December 2000	Pearson's correlation		0.90	13.77	<0.001	48	46
Alg089	January 2001	Pearson's correlation		0.48	3.65	<0.001	53	51
Alg091	February 2001	Pearson's correlation		0.85	11.52	<0.001	53	51
Alg094	April 2001	Pearson's correlation		0.92	16.67	<0.001	54	52
Alg096	June 2001	Pearson's correlation		0.64	5.60	<0.001	47	45
Alg107	June 2002	Pearson's correlation		0.97	28.25	<0.001	54	52
Alg118	December 2002	Pearson's correlation		0.67	6.44	<0.001	53	51
Afr179	June 2003	Pearson's correlation		0.69	6.30	<0.001	46	44
Alg131	September 2004	Pearson's correlation		0.83	10.19	<0.001	50	48
Afr202	December 2004	Spearman's rank correlation	0.40			<0.05	37	30
Afr219	June 2005	Spearman's rank correlation	0.54			<0.001	42	40
Afr222	August 2006	Pearson's correlation		0.89	12.36	<0.001	41	39
Afr224	September 2006	Pearson's correlation		0.83	9.83	<0.001	45	43
Afr230	February 2007	Spearman's rank correlation	0.78			<0.001	27	25

### Particle size data

#### Chlorophyll a maximum particle spectra

A total of 171 stations were sampled. A subsurface chlorophyll a maximum was observed at 54% of all stations sampled. A decrease in particle concentration from the surface to the chlorophyll a maximum was observed at 20% of all stations sampled and an increase in particle concentration from the surface to the chlorophyll a maximum was observed at 34% of all stations sampled. A surface chlorophyll a maximum was observed at 46% of all stations sampled. Therefore, 66% of stations either had a surface chlorophyll a maximum or subsurface chlorophyll a maximum with a surface particle concentration maximum (Table 3). Surface samples were used in later analyses because they were more likely to typify the phytoplankton community.

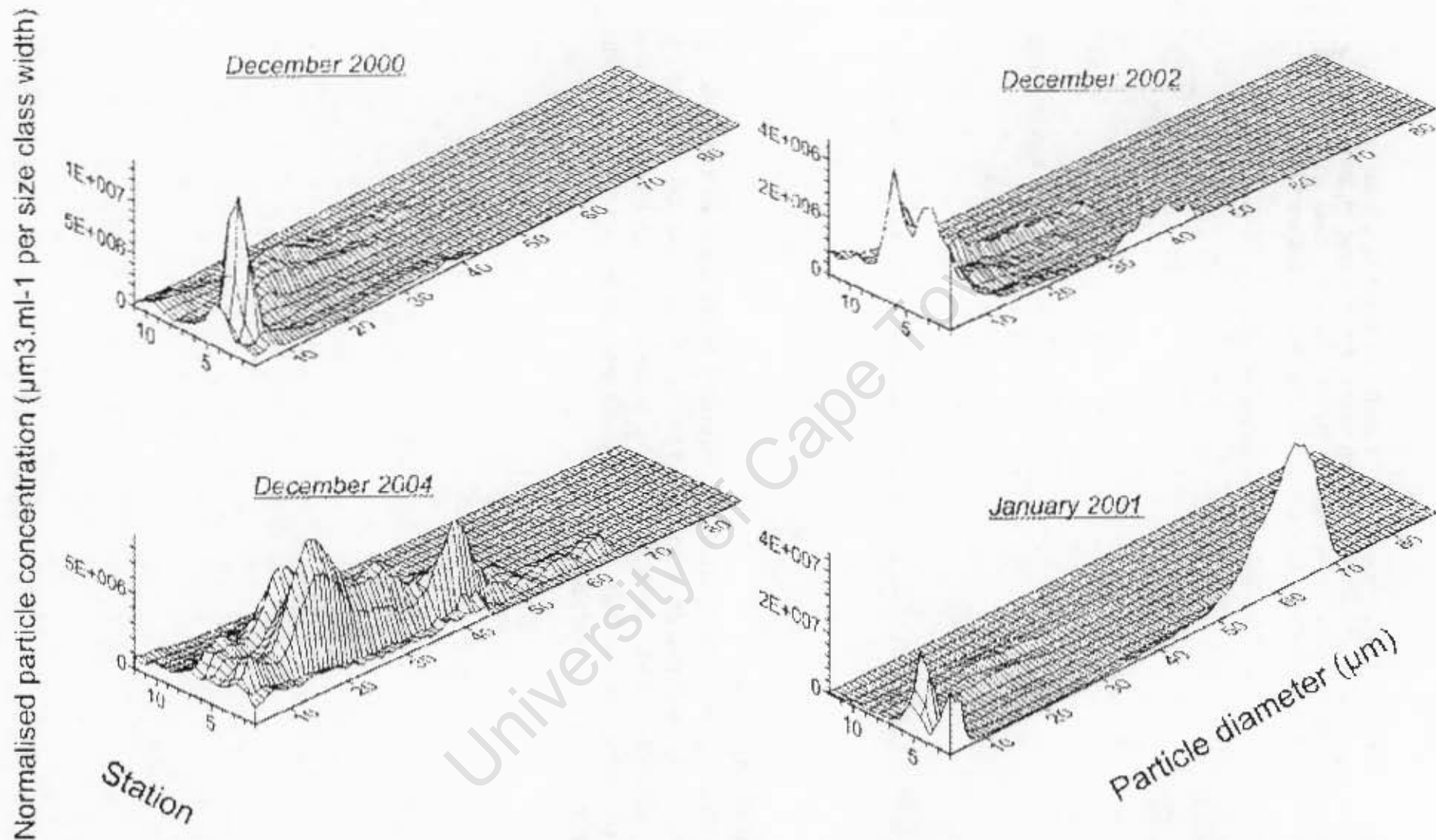
**Table 3** Direction of change in total particle concentration (by volume) between surface samples and chlorophyll a maximum samples for each station of each cruise. Hyphens indicate a surface chlorophyll a maximum and arrows indicate the increase or decrease at stations with subsurface chlorophyll a maxima. Greyed out blocks indicates stations that were not sampled.

Cruise/ Station	Direction of change in total particle volume from surface to chlorophyll a maximum											
	1	2	3	4	5	6	7	8	9	10	11	12
September 2000	-	-	-	-	↓	↑	↓	-	↑	↑	↓	-
December 2000	-	-	-	-	↓	↑	↑	↑	↓	↑	↑	-
January 2001	-	-	↓	↓	↓	↓	↓	-	↑	↑	-	↑
February 2001	-	-	↑	↑	-	↑	-	-	↓	↓	↑	↑
April 2001	-	-	↑	↑	-	-	-	↑	-	↑	-	-
June 2001	-	-	↑	↑	-	-	-	↑	↑	↑	-	-
June 2002	↑	↑	↑	↑	-	-	-	-	↑	↑	↑	↑
December 2002	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑
June 2003	-	-	-	-	-	↓	↓	↓	↓	-	-	-
September 2004	-	-	-	-	-	↑	↓	↑	↑	↑	↓	↑
December 2004	↑	-	↓	↓	-	-	-	-	↓	-	↓	-
June 2006	-	↓	↑	↑	↑	-	-	-	↑	↑	↑	-
August 2006	-	-	↓	↓	-	-	-	↓	-	-	-	-
September 2006	-	-	↑	↓	-	↓	-	↓	↓	↓	-	↑
February 2007	-	-	↓	-	-	-	-	-	↑	↓	↓	↓

### Surface particle spectra

Particle size data (Figure 5) are reported on a cruise by cruise basis with reference to upwelling events (Figure 3) and the temperature profiles of the cruise (See Appendix B for profiles). Similarities and differences among cruises are also highlighted. The descriptions of particle spectra from each cruise are ordered by month, starting with summer months, then chronologically.





**Figure 5** Three dimensional plots of particle size data analysed by the Coulter Counter of surface samples from each cruise. The particle concentration has been normalised per size class width (z-axis). Station number is on the y-axis and particle diameter is on the x-axis. The lower particle limit is 4  $\mu\text{m}$  ESD. Size classes with particle counts less than 10 were set to zero. Cruises are ordered chronologically and summer months first, left to right and top to bottom. Particle spectra for the 5<sup>th</sup> to 15<sup>th</sup> cruise are in panels below.

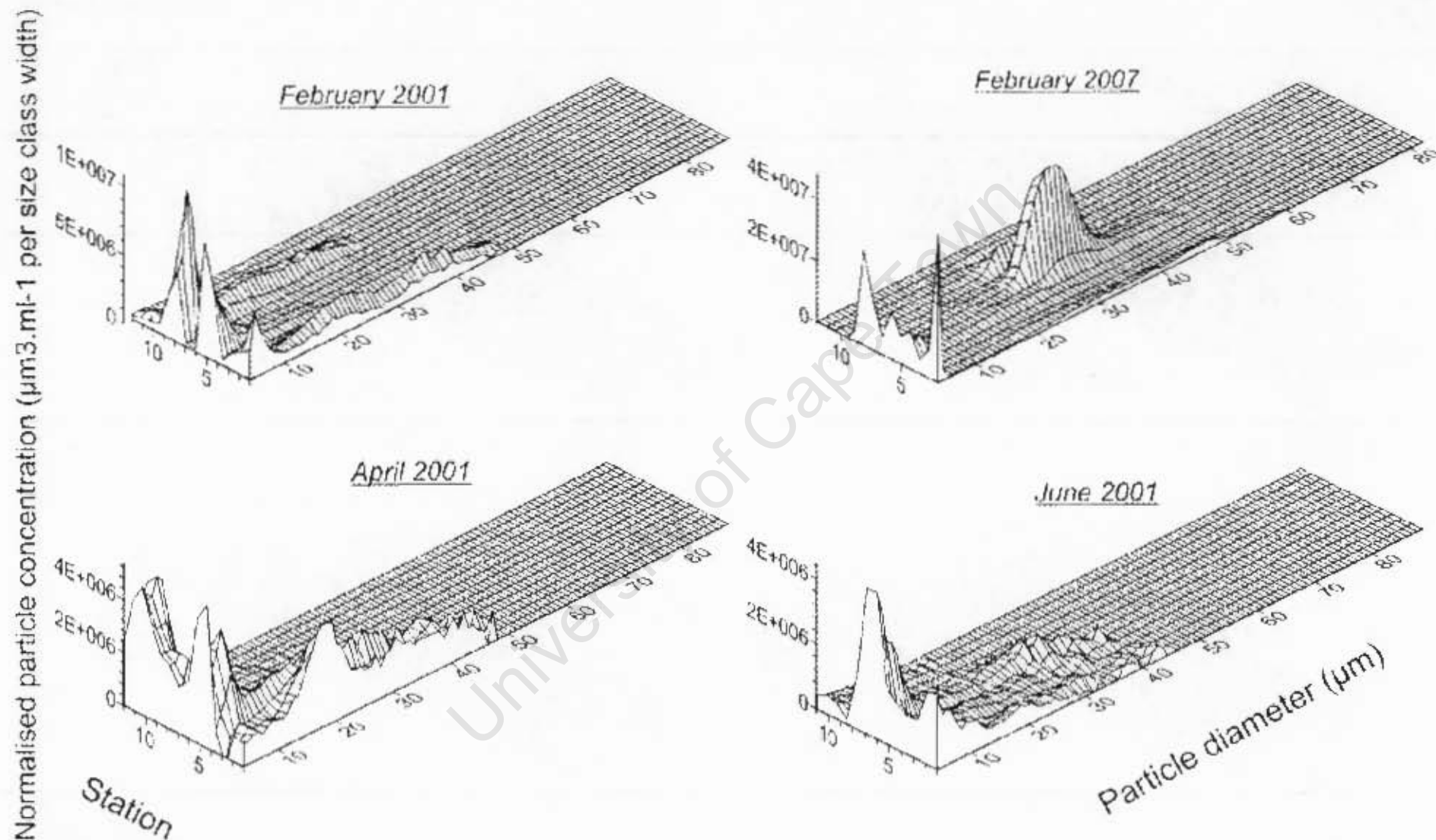
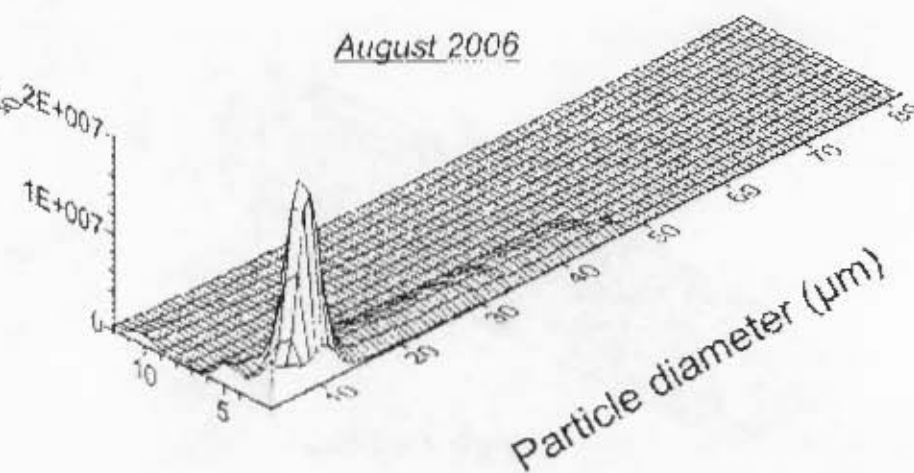
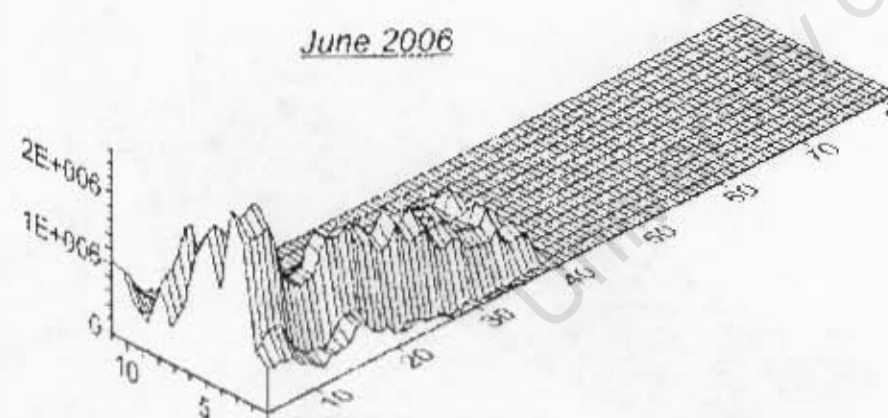
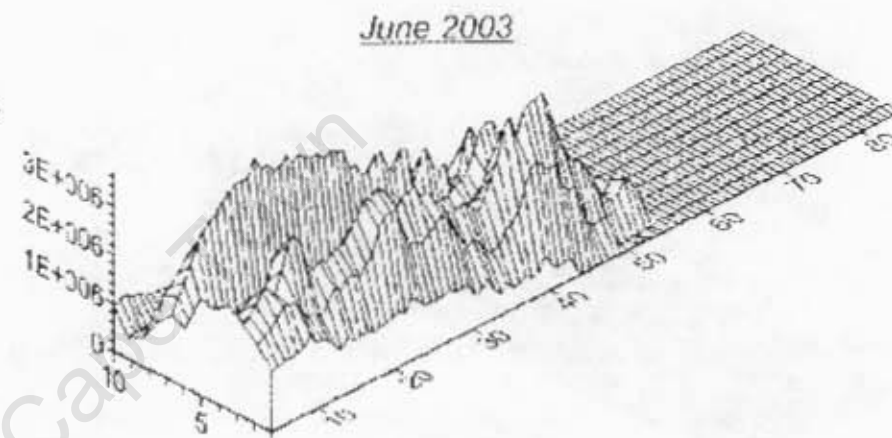
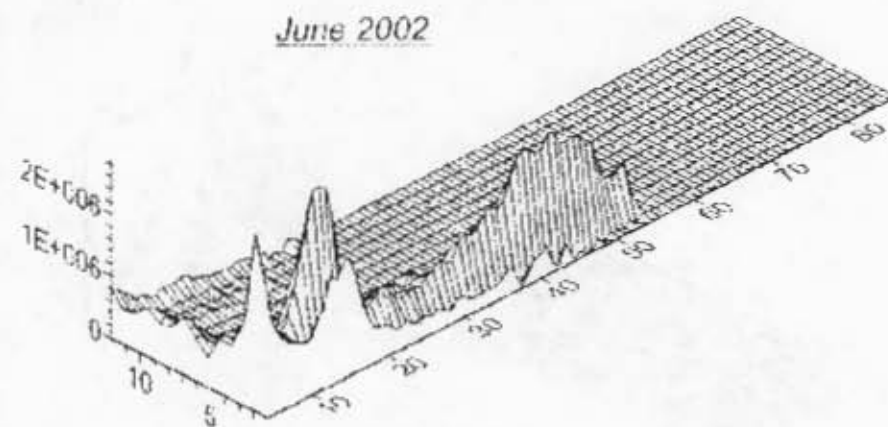


Figure5 (continued)

Normalised particle concentration ( $\mu\text{m}^3\cdot\text{ml}^{-1}$  per size class width)



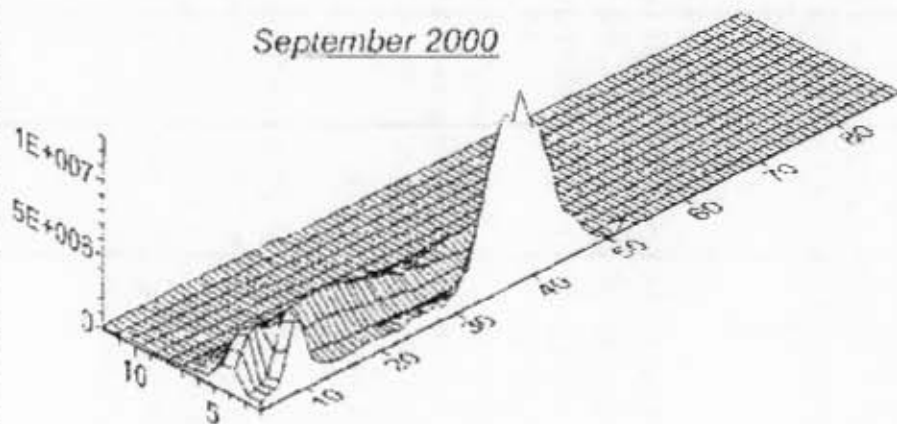
Station

Particle diameter ( $\mu\text{m}$ )

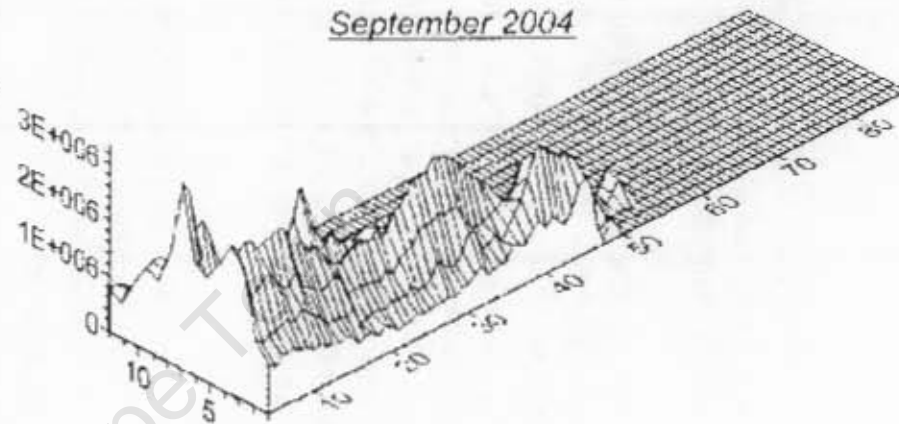
Figure5 (continued)

Normalised particle concentration ( $\mu\text{m}^3\cdot\text{ml}^{-1}$  per size class width)

September 2000



September 2004



September 2006

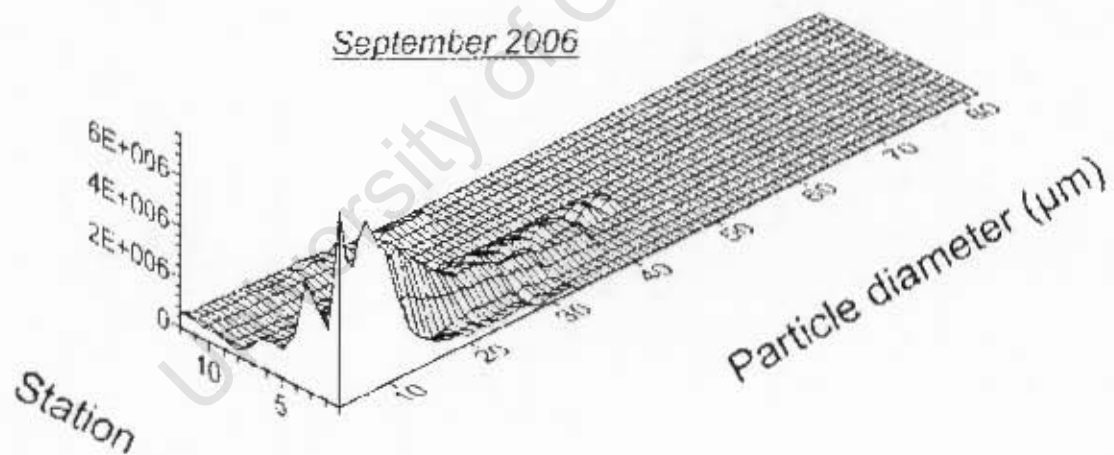


Figure5 (continued)

### **December 2000**

Sustained powerful upwelling occurred, similar to the situation in December 2004. A large upwelling event commenced 19 days prior to the cruise and the cumulative divergence of that event was  $1713.98 \text{ m}^2.\text{s}^{-1}$  on the day of sampling.

A bloom of large cells ( $20 - 45 \text{ }\mu\text{m}$  ESD) persisted at Station 1 and 2 where water temperature was uniform ( $< 10 \text{ }^\circ\text{C}$ ). A bloom of small cells ( $5 - 10 \text{ }\mu\text{m}$  ESD) dominated the particle spectra at stations 1 to 5; the concentration increasing to Station 5. A low concentration peak at  $10 - 20 \text{ }\mu\text{m}$  ESD was also observed at Station 5. This peak became dominant offshore at stations 6 to 8, where active upwelling caused waters to be well-mixed in the upwelling plume. Large cells (up to  $45 \text{ }\mu\text{m}$  ESD) were present at stations 6 to 8. Large cells became less prevalent and particle spectra were dominated by cells less than  $10 \text{ }\mu\text{m}$  ESD offshore of Station 8 where waters were warm ( $18 - 19 \text{ }^\circ\text{C}$ ) and highly stratified. The maximum fluorescence values coincided with the maximum particle concentration at stations 6 to 8.

Observations are consistent with what is expected from size-based theory. Nutrient-rich water in the upwelling plume (stations 6 to 8) allowed intermediate-sized cells to develop. Offshore of the upwelling front insufficient nutrients were present and small cells dominated particle spectra. Cyclonic circulation of cold nutrient-rich water to inshore stations allowed a bloom of even larger cells to develop without being flushed out. However, larger cells were expected to dominate particle spectra in the inner bay (stations 1 to 3). Zooplankton grazing could have possibly restrained the population to a low concentration.

### **December 2002**

Weak upwelling conditions occurred prior to sampling. Three upwelling events occurred within 20 days prior to the cruise. The first upwelling event lasted nine days, the second upwelling event lasted three days (from eight to 10 days prior) and the third upwelling event lasted one day. The cumulative divergence for each event was 571.46, 240.96 and  $5.19 \text{ m}^2.\text{s}^{-1}$ , respectively. Downwelling persisted for two days prior to sampling. Waters were well-mixed at stations 8 to 12 and the surface temperature was approximately  $16 \text{ }^\circ\text{C}$ . A shallow upper mixed layer was well-developed at the inner stations. Waters became progressively more mixed moving offshore.

Surface waters were warming and a strong thermocline had developed inshore. A remnant growth of large cells persisted at Station 1 ( $30 - 45 \text{ }\mu\text{m}$  ESD) at a relatively low concentration. Large cells (up to  $32 \text{ }\mu\text{m}$  ESD) persisted again at Station 7, but small cells less than  $10 \text{ }\mu\text{m}$  ESD dominated the particle spectra, cells less than  $5 \text{ }\mu\text{m}$  ESD double the concentration of cells  $5 - 10 \text{ }\mu\text{m}$  ESD. The maximum cell size was  $21 \text{ }\mu\text{m}$

ESD and total particle concentration dropped offshore of Station 7 even though waters were more mixed than stations inshore. Cells less than 10  $\mu\text{m}$  ESD dominated these particle spectra, the concentration of cells less than 5  $\mu\text{m}$  ESD almost double those 5 – 10  $\mu\text{m}$  ESD.

The available data does not describe the hydrographic processes adequately to explain the absence of large cells in well-mixed water of the outer stations. Quite possibly, particle spectra represent a late stage successional bloom, after nutrients have been removed from the water and dominance has switched back to small cells. Alternatively, mixing reduced light levels and limited growth of larger cells. Large cells were expected to dominate at the inner bay and frontal area, however small cells dominated the particle spectra.

#### ***December 2004***

Upwelling was of moderate strength, uninterrupted and slightly weaker than in December 2000. An upwelling event commenced 11 days prior to sampling and the cumulative divergence of that event one day prior to sampling was  $728.32 \text{ m}^2.\text{s}^{-1}$ . The position of the front was between Station 7 and Station 9.

A bloom of cells less than 10  $\mu\text{m}$  ESD dominated the particle spectra of Station 1 where waters were less than  $10^\circ\text{C}$ . A growth of large cells (35 – 47  $\mu\text{m}$  ESD), possibly dinoflagellates, were present at low concentration inshore at Station 1 and dominated the particle spectra at Station 2. Active upwelling of nutrients allowed a bloom of intermediate-sized cells (10 to 32  $\mu\text{m}$  ESD) to dominate the particle spectra at stations 3 to 9. The concentration of the bloom peaked at Station 5 and its next highest concentration was in the upwelling plume, at Station 7. Particle spectra data for Station 10 are unavailable. Beyond the upwelling front (stations 11 and 12) cells less than 10  $\mu\text{m}$  ESD dominated the particle spectra.

The pattern of cell dominance is expected from size-based theory. Active upwelling of nutrient-rich water allows intermediate-sized cells to persist in the upwelling plume, beyond the upwelling front insufficient nutrients influx and small cells dominate the spectra. Inshore of the upwelling plume cyclonic circulation and a more stable water column, favoured the domination of intermediate cells, a mid-stage successional type bloom. The dominance of small cells at Station 1 was not expected. Possibly, local reseedling of small cells occurred or the small cells responded quickly to a patch of coastal upwelling.

### ***January 2001***

Upwelling favourable conditions lasted for eight days prior to sampling and cumulative divergence reached  $620.09 \text{ m}^2.\text{s}^{-1}$ . A large upwelling event ended 13 days prior to sampling, the cumulative divergence of the event was  $3090.67 \text{ m}^2.\text{s}^{-1}$ . Upwelling was less powerful than in December 2000.

A mature bloom of very large cells ( $50 - 70 \text{ }\mu\text{m}$  ESD) dominated the particle spectra at Station 2, and was not observed at any other stations. The maximum particle size at other stations was  $45 \text{ }\mu\text{m}$  ESD. Cells less than  $10 \text{ }\mu\text{m}$  ESD dominated particle spectra inshore of Station 6 (except at Station 2) and the concentration increased to Station 5. Active upwelling and an intermediate-sized bloom ( $11 - 27 \text{ }\mu\text{m}$  ESD) persisted at relatively moderate concentrations at Station 6 and dominated particle spectra at stations 7 and 8 and persisted at Station 9, in the upwelling plume, the same as in December 2000 and December 2004. The maximum size of cells at the outer three stations was  $25 \text{ }\mu\text{m}$  ESD and small cells less than  $10 \text{ }\mu\text{m}$  ESD dominated the particle spectra. Particle spectra were relatively low from Station 9 onwards. CTD data for stations 8 to 12 are not available.

The dominance of intermediate-sized cells in the upwelling plume is expected because of sufficient availability of nutrients, offshore of the plume waters are warm, stratified and nutrient-depleted and small cells dominate. Larger cells are expected to dominate the inner bay (stations one to three); however nutrient depletion may have limited their growth.

### ***February 2001***

Upwelling ceased three days prior to sampling, before that a moderately powerful upwelling event commenced 23 days prior to sampling. The cumulative divergence of that event was  $1303.49 \text{ m}^2.\text{s}^{-1}$ . Upwelling re-commenced two days prior to sampling, the cumulative divergence was  $108.09 \text{ m}^2.\text{s}^{-1}$  on the day of sampling.

There was a dominance of small cells ( $< 10 \text{ }\mu\text{m}$  ESD) inshore at Station 1, at stations 3 to 8 and at stations 10 to 12. The waters at stations 10 to 12 were warm ( $> 20 \text{ }^{\circ}\text{C}$ ) and the upper mixed layer extended to below 40 m, whereas at the inner stations the upper mixed layer was less than 20 m. This bloom peaked at Station 8, in the outer edge of the Columbine plume, and then rapidly declined offshore. A mixture of cells  $10 - 27 \text{ }\mu\text{m}$  ESD and  $27 - 49 \text{ }\mu\text{m}$  ESD occurred at Station 1 and dominated the spectrum at Station 2. The  $27$  to  $49 \text{ }\mu\text{m}$  ESD peak also dominated at Station 9, but was completely absent from the outer stations and at stations 3 to 8.



The upwelling data indicates active upwelling but the prevalence of intermediate-sized cells is less than expected. A cessation of upwelling results in a shoreward movement of surface water as the wind stress is relieved, the offshore piling up of water slops back towards the coast, aggregating cells in the near shore which explains the presence of large cells at stations 1 and 2. At stations 4 to 8 the thermocline was well-developed and the mixed layer deeper. Upwelling commenced three days prior to sampling, so it is possible that there was insufficient time for large cells to grow to dominance. There is a possible beginning of a large-celled bloom at Station 9. Small cells which divide and take up nutrients rapidly dominated. Although CTD data are unavailable for Station 9, it was quite possibly a frontal station with accumulation of some cells.

### **February 2007**

Two upwelling events occurred within 20 days prior to sampling. The first event was moderate; commenced 19 days before sampling, lasted 13 days and the cumulative divergence was  $941.37 \text{ m}^2.\text{s}^{-1}$ . The second upwelling event, commenced three days before sampling, the cumulative divergence was  $110.50 \text{ m}^2.\text{s}^{-1}$  on the day of sampling. At all stations solar warming had increased the temperature of the surface waters and stratification was present, indicating that the second upwelling event was not a surface feature on the day of sampling. However, at Station 8 active upwelling might have recently ceased because surface warming was shallow. The upper mixed layer at Station 6 was also shallow. Otherwise, the upper mixed layer deepened moving offshore. The surface temperature increased moving offshore from  $11.49^\circ\text{C}$  at Station 1 to  $21.80^\circ\text{C}$  at Station 12 with a frontal zone between Station 8 and Station 10.

A bloom of cells from 22 to  $40 \mu\text{m}$  ESD persisted at Station 6 and dominated at Station 7. The concentration of these cells then decreased at Station 8, but dominated again at stations 9 and 10. An intermediate-sized growth of cells ( $12 - 40 \mu\text{m}$  ESD) also persisted at a low concentration at Station 3. Particle spectra of the outer two stations (11 and 12) were low and flat with cells less than  $20 \mu\text{m}$  ESD present. Otherwise, stations were dominated by cells less than  $10 \mu\text{m}$  ESD. The concentration of these cells peaked at stations 1 and 8.

It is expected that larger cells dominate in the upwelling plume (stations 6 to 8) and small cells dominate outside the plume. Stations inside of the upwelling plume were also stratified and small cells dominated. Localised seeding was probably responsible for the isolated growth of 22 to  $40 \mu\text{m}$  ESD cells at Station 3. Larger cells were expected to be more prevalent inshore; they were possibly grazed to a low concentration by zooplankton.



### **April 2001**

A 53 day upwelling event reached a cumulative divergence of  $3663.07 \text{ m}^2.\text{s}^{-1}$  prior to sampling. There was no upwelling two days prior to sampling. The large upwelling event is split into three sections where divergence dropped temporarily, indicated by constant cumulative divergence. Waters were well-mixed; stratification of the upper layer was not observed, although inshore waters were stabilising, indicative of aged upwelled water. The upwelling front was between stations 5 and 7.

A bloom of intermediate-sized cells ( $10 - 22 \text{ }\mu\text{m}$  ESD) dominated and a growth of large cells ( $22 - 47 \text{ }\mu\text{m}$  ESD) persisted at approximately half the concentration of the intermediate-sized cells at stations 1 to 3. Small cells (less than  $10 \text{ }\mu\text{m}$  ESD) dominated at stations 4 to 12, a peak of cells between  $5$  and  $7 \text{ }\mu\text{m}$  ESD. Large cells ( $> 30 \text{ }\mu\text{m}$  ESD) did not persist beyond Station 4.

The dominance of intermediate-sized cells in the inner bay (stations 1 to 3) is expected because of recirculation of recently upwelled water that has stabilised and allows growth of larger cells. Small cells are expected to dominate in the frontal area and offshore because quiescent, nutrient-poor conditions prevailed. Small cells respond quickly to conditions after cessation of upwelling.

### **June 2001**

Downwelling conditions prevailed for seven days prior to sampling. The cumulative divergence for two upwelling events that occurred within 20 days prior to sampling was  $52.26$  and  $21.82 \text{ m}^2.\text{s}^{-1}$ . The water column was stratified at all stations. Surface water was between  $14$  and  $14.6 \text{ }^{\circ}\text{C}$  at the inner stations and warmer at the outer five stations ( $16.4 - 17.6 \text{ }^{\circ}\text{C}$ ). The upper mixed layer depth ranged between  $25$  and  $38.7 \text{ m}$  at the inner stations and below  $44 \text{ m}$  at the outer stations. The front was between stations 7 and 8.

A low concentration of cells between  $20$  and  $40 \text{ }\mu\text{m}$  ESD persisted from stations 1 to 7; cells up to  $44 \text{ }\mu\text{m}$  ESD were present. The proportionate contribution of these large cells was the largest at Station 5, 6 and 7. However, small cells ( $< 10 \text{ }\mu\text{m}$  ESD) dominated throughout the transect. The total particle concentration peaked at Station 6 and Station 7, as did fluorescence.

The dominance of small cells is expected under quiescent upwelling conditions where the lack of nutrients favours the growth of small cells. However, sufficient nutrients probably existed for cells  $20$  to  $40 \text{ }\mu\text{m}$  ESD to persist at a low concentration. These larger cells were not present at the warmer more stratified water of stations 8 to 12 probably due to mixing with oceanic water.

### **June 2002**

A three day upwelling event commenced 20 days prior to sampling and reached a cumulative divergence of  $130.73 \text{ m}^2\text{s}^{-1}$ . Upwelling recommenced two days prior to sampling but was interrupted on the first day of sampling. Water at stations 6 to 12 was warmer ( $> 15^\circ\text{C}$  at the surface) and more stratified than stations 3 to 5. The upper mixed layer depth was below 30 m. The water column at stations 3 to 5 was less stable than at the stations 6 to 12, an upper mixed layer was not well-developed. CTD data are unavailable for stations 1 and 2.

An intermediate-sized bloom peaking at  $15 \mu\text{m}$  ESD (from  $10$  to  $20 \mu\text{m}$  ESD) dominated surface particle spectra at stations 1 and 3, and at the chlorophyll maximum at Station 2. Cells less than  $8 \mu\text{m}$  ESD dominated at the surface. A bloom of large cells ( $30$  to  $56 \mu\text{m}$  ESD) also persisted at Station 3. The prevalence of large size classes decreased offshore of Station 5 and small cells ( $< 10 \mu\text{m}$  ESD) dominated at all other stations. Cells less than  $20 \mu\text{m}$  ESD persisted at stations 6 to 11.

The dominance of intermediate cells in the inner bay is expected because the recirculation of recently upwelled water. Mixing of water at these inner stations most likely increased the influx of nutrients to the euphotic zone, decreased the rate of sedimentation and moved seed cells upward contributing to the persistence of large-celled phytoplankton (Kiørboe, 1993; Arin, 2002). The dominance of small cells is expected at stations 6 to 12 because following the cessation of upwelling waters were warm, stratified and most likely nutrient-depleted.

Fluorescence was highest at the inner three stations and total particle concentration also peaked at stations 1 to 3, an indicator that particles represented majority phytoplankton cells.

### **June 2003**

Four upwelling events occurred within 20 days prior to sampling. The largest event reached a cumulative divergence of  $121.68 \text{ m}^2\text{s}^{-1}$ . Downwelling conditions prevailed one day prior to sampling and on sampling days. Waters were well-mixed at stations 1 to 3 and the surface temperature was between  $11$  and  $12^\circ\text{C}$ . Water at stations 8 and 9 were warm (surface at  $17.7^\circ\text{C}$ ) and highly stratified. The upper mixed layer depth was at  $43.7 \text{ m}$ . CTD data are not available near the surface for stations 4 to 7 and for stations 11 and 12, but it appears that the front was between stations 7 and 8.

A bloom of large cells ( $34 - 50 \mu\text{m}$  ESD) persisted at stations 1 to 7 and dominated the particle spectra at stations 3 to 5. At Station 6 and Station 7 cells between  $10$  and  $30$

$\mu\text{m}$  ESD dominate the spectra. At Station 6 a relatively low particle concentration was observed which coincided with the lowest fluorescence values. Offshore of Station 8 surface waters were warm and highly stratified and small cells ( $< 10 \mu\text{m}$  ESD) dominated the particle spectra, although large cells up to  $32 \mu\text{m}$  ESD persisted. Particle samples were not collected for Station 11 and Station 12 on this occasion.

Dominance of intermediate to large cells from stations 1 to 7 is expected because of the recirculation of upwelled nutrient-rich water that is stabilising and ageing. It is probable that turbulence also decreased the rate of sedimentation of the large cells. The dominance of small cells offshore (stations 9 to 12) is also expected because the warm stratified water was most likely nutrient-depleted. Lateral mixing of older surface waters following brief and less intense upwelling events may be responsible for the persistence of larger cells offshore in warm stratified water. The available data does not explain the inconsistency.

### **June 2006**

Three upwelling events occurred within 20 days prior to sampling. The cumulative divergence of each event was 4.66, 152.93 and  $191.73 \text{ m}^2.\text{s}^{-1}$ , respectively. Upwelling was interrupted seven days prior to sampling and one day prior to sampling. Water at stations 9 to 12 was warm (surface water between  $15$  and  $16^\circ\text{C}$ ) and highly stratified, the upper mixed layer depth extended to below  $40 \text{ m}$  at these stations. Surface water at stations 1 to 8 was between  $13$  and  $14^\circ\text{C}$ . The water at stations 7 and 8 was well-mixed whereas water at stations 3 to 6 was more stable. The upper mixed layer depth was between  $30$  and  $40 \text{ m}$  at stations 3 to 6. No upper mixed layer was observed at stations 1 and 2. The front was between Station 8 and Station 9.

A bloom of small cells ( $< 10 \mu\text{m}$  ESD) was dominant at all the stations, the concentration peaking at Station 3 and only decreasing substantially after Station 8. The contribution of cells  $10$  to  $30 \mu\text{m}$  ESD to the particle spectra increased to Station 3 but decreased afterwards. The conditions favoured the persistence of a bloom of intermediate ( $10 - 30 \mu\text{m}$  ESD) and large cells (up to  $30 - 40 \mu\text{m}$  ESD) at stations 6 to 8. The intermediate-sized cells also persisted inshore at stations 1 and 2. Cells less than  $20 \mu\text{m}$  ESD persisted at stations 9 to 11 where surface waters were warmer and had a deeper upper mixed layer.

The dominance of small cells is expected at stations 9 to 11 where water was warm and highly stratified and most likely nutrient-depleted. The persistence of intermediate-sized cells at the middle stations is also expected because waters were well-mixed following the upwelling event. Stabilisation of the water column at the inner stations had also allowed the persistence of large cells. Dominance of small cells at these stations

was not expected but possibly occurred because there were insufficient nutrients for larger cells to bloom.

### **August 2006**

Five upwelling events occurred within 20 days prior to sampling. The largest event commenced three days before the cruise, the cumulative divergence of that event was  $288.87 \text{ m}^2.\text{s}^{-1}$  on the day of sampling. From stations 6 to 12 surface water was between 13 and 16 °C and the water column was highly stratified, the upper mixed layer depth was below 40 m. Water at stations 3 to 5 were less stable, a uniform upper layer was present in the upper 20 m. No thermocline was observable at Station 1 and Station 2.

Small cells less than 10 µm ESD dominated particle spectra at all stations except stations 3 and 4. A mature bloom of small cells (10 µm ESD) persisted inshore and dominated particle spectra at stations 3 and 4. Large cells (up to 47 µm ESD) persisted at these stations but at low concentration. Highly stratified water presented low and relatively flat spectra at stations 6 to 8. Cells less than 23 µm ESD persisted at the outer three stations. From Station 5 to Station 6 the upper mixed layer deepened considerably, from 20 m to 60 m. The particle concentration more than halved between the stations and the relative contribution of cells between 10 to 20 µm ESD increased.

Larger cells were expected to dominate the inner bay to the front (stations 1 to 5) because cyclonic circulation of upwelled water and relatively stable waters should have allowed larger cells to persist. The sedimentation of large cells from the euphotic zone following stabilisation of the water column is a possible explanation for the absence of large cells at the surface. The dominance of small cells observed at the outer stations is expected because waters were warm and stratified.

### **September 2000**

Two upwelling events occurred within 20 days prior to sampling, the cumulative divergence of those events was 295.62 and 70.30  $\text{m}^2.\text{s}^{-1}$ , respectively. Upwelling was interrupted for nine days after the first event. Downwelling conditions persisted for two days prior to sampling. Upwelling on the day of sampling was not intense; the cumulative divergence was 13.73  $\text{m}^2.\text{s}^{-1}$ . The outer stations (7 to 12) were warm and highly stratified; the surface temperature was between 16 and 17 °C. Surface water at stations 1 to 5 was colder (13 to 15 °C) and the upper mixed layer depth was above 20 m, except at Station 5 which was at 27 m.

A small-celled bloom (4 – 11 µm ESD) persisted at stations 2 to 5, and dominated at stations 3 and 4. A large-celled bloom (30 – 46 µm ESD) dominated the particle spectra at Station 2, the concentration more than double the small peak. An intermediate-sized

bloom (approximately 10 – 20  $\mu\text{m}$  ESD) dominated particle spectra at stations 5, 6 and 7. Small cells dominated the chlorophyll maximum spectra at Station 7. The large-celled bloom also persisted at a low concentration at Station 6. Relatively flat spectra were present offshore of Station 6. Cells less than 10  $\mu\text{m}$  ESD dominated particle spectra from stations 8 to 10. No particle peaks were present at Station 11 and Station 12 and cells up to 27  $\mu\text{m}$  ESD were persisted.

The dominance of small cells at stations 7 to 12 is expected because the water is warm and stratified and most likely nutrient-poor. Small cells were also expected to dominate the inner stations because of prevailing downwelling conditions and stratification of the water column. The onshore movement of water following relaxation of upwelling and recirculation of recently upwelled water is a possible explanation for the dominance of large cells.

#### **September 2004**

Four weak upwelling events occurred within 20 days prior to sampling. The largest of the events commenced 26 days prior to sampling, lasted eight days and the cumulative divergence of that event was  $350.57 \text{ m}^2.\text{s}^{-1}$ . Upwelling was repeatedly interrupted 12, seven and five days prior to sampling. Continuous upwelling occurred for four days prior to sampling, reaching a cumulative divergence of  $367.37 \text{ m}^2.\text{s}^{-1}$  on the day of sampling. Waters were mixed throughout the water column at stations 5 to 12. Stratification was present at stations 1 to 4; the upper mixed layer was less than 20 m. The upwelling front was present between Station 8 and Station 9.

Four different sized blooms persisted along the transect. The largest (35 – 48  $\mu\text{m}$  ESD) dominated at inner two stations. A 24 – 35  $\mu\text{m}$  ESD bloom persisted at stations 3 and 4 and cells less than 10  $\mu\text{m}$  ESD dominated the spectra from stations 3 to 12, except at Station 8 which was dominated by 20  $\mu\text{m}$  ESD peak. The prevalence of large cells decreased moving offshore.

Blooms of intermediate-sized cells are expected under active upwelling in the upwelling plume (stations 6 to 8) because of increased turbulence and the influx of nutrients, however it was not observed. The persistence of the intermediate- and large-sized peaks at isolated stations is difficult to explain from the upwelling and temperature data, considering water was well-mixed from stations 1 to 8. Again, it is possible that mixing of phytoplankton blooms associated with nearby water and local reseeded occurred. Deep winter mixing could possibly have reduced light levels so that large cells could not persist.

### **September 2006**

Upwelling commenced nine days before sampling, but was interrupted five days prior to sampling. The cumulative divergence was  $661.71 \text{ m}^2.\text{s}^{-1}$ . Upwelling recommenced two days prior to sampling; the cumulative divergence was  $154.14 \text{ m}^2.\text{s}^{-1}$  on the day of sampling. The upper mixed layer deepened considerably at stations 8, 9 and 10, temperature in the upper 60 m of the water column was uniform ( $15 - 16^\circ\text{C}$ ) at stations 8 to 10. The upper mixed layer depth was shallower at stations 6 and 7 and waters were well-mixed at the inner five stations. CTD data are unavailable for Station 11 and Station 12.

A bloom of cells less than  $10 \mu\text{m}$  ESD dominated inshore at stations 1 to 3. A bloom of intermediate-sized cells ( $10 - 20 \mu\text{m}$  ESD) dominated particle spectra at stations 4 to 7; cells up to  $46 \mu\text{m}$  ESD persisted. The contribution of large cells to particle spectra increases from stations 1 to 5. The particle spectra at stations 8 to 12 were relatively flat, however small cells ( $< 10 \mu\text{m}$  ESD) were more prevalent at the stations 8 to 10. Larger particles also persisted (up to  $33 \mu\text{m}$  ESD at Station 11) and the relative contribution of cells  $10$  to  $20 \mu\text{m}$  ESD increased moving offshore from Station 7. Total particle concentration decreased by a third from Station 7 to Station 8. This pattern occurred for the previous month. In August 2006 there was also an increased prevalence of large cells offshore and a sudden deepening in the upper mixed layer.

The intermediate-sized bloom is expected at stations 4 to 7 because upwelling has been active and the water column is stable enough to retain these cells at the surface. Mixing along with possible recirculation and ready seeding which allows small cells to respond quickly to fresh injections of nutrients may explain the dominance of small cells inshore at stations 1 to 3. It was unexpected to observe cells up to  $33 \mu\text{m}$  ESD albeit at a low concentration in highly stratified water at the outer three stations. What can happen across the whole ocean at these latitudes is there is a weak "spring bloom" if conditions allow the upper mixed layer to stabilize as light levels increase. There are moderate nutrient levels following the winter mixing so large cells can occur way offshore, beyond the influence of upwelling (Pers. Comm. L. Hutchings). Alternatively, there was a moderately powerful upwelling event that finished six days before sampling; possibly the large cells was a remnant bloom from the previous upwelling event. Phytoplankton dynamics and multiple upwelling events can produce considerable complexity when expressed in terms of particle spectra.

### **Expected size distribution**

Particle spectra collected on individual cruises during summer months conformed to the expected size distribution on 17% of samples from the inner bay, 67% of samples from the frontal area and 100% of samples from offshore stations (Table 4). There were no

cruises undertaken in summer during which the observed size distributions conformed to the expected size distribution at all stations of the transect (Table 4). Particle spectra collected during winter months conformed to the expected size distribution 56% of the time. In winter, observed particle spectra from the inner bay and offshore stations conformed to the expected size distribution on 89% and 100% of occasions, respectively, whereas particle spectra from the frontal area conformed to the expected size distribution 67% of the time (Table 4).

Forty-one observations were evaluated using the expert system, 31 of those observations (78%) conformed to the expected size distribution predicted using upwelling and temperature data. Results were as expected except for a situation of active upwelling three days before the cruise where cells could be smaller than expected in the inner bay and for a situation in the frontal area of multiple upwelling events 11 days prior to the cruise where cells were also smaller than expected (figure 6).

University of Cape Town

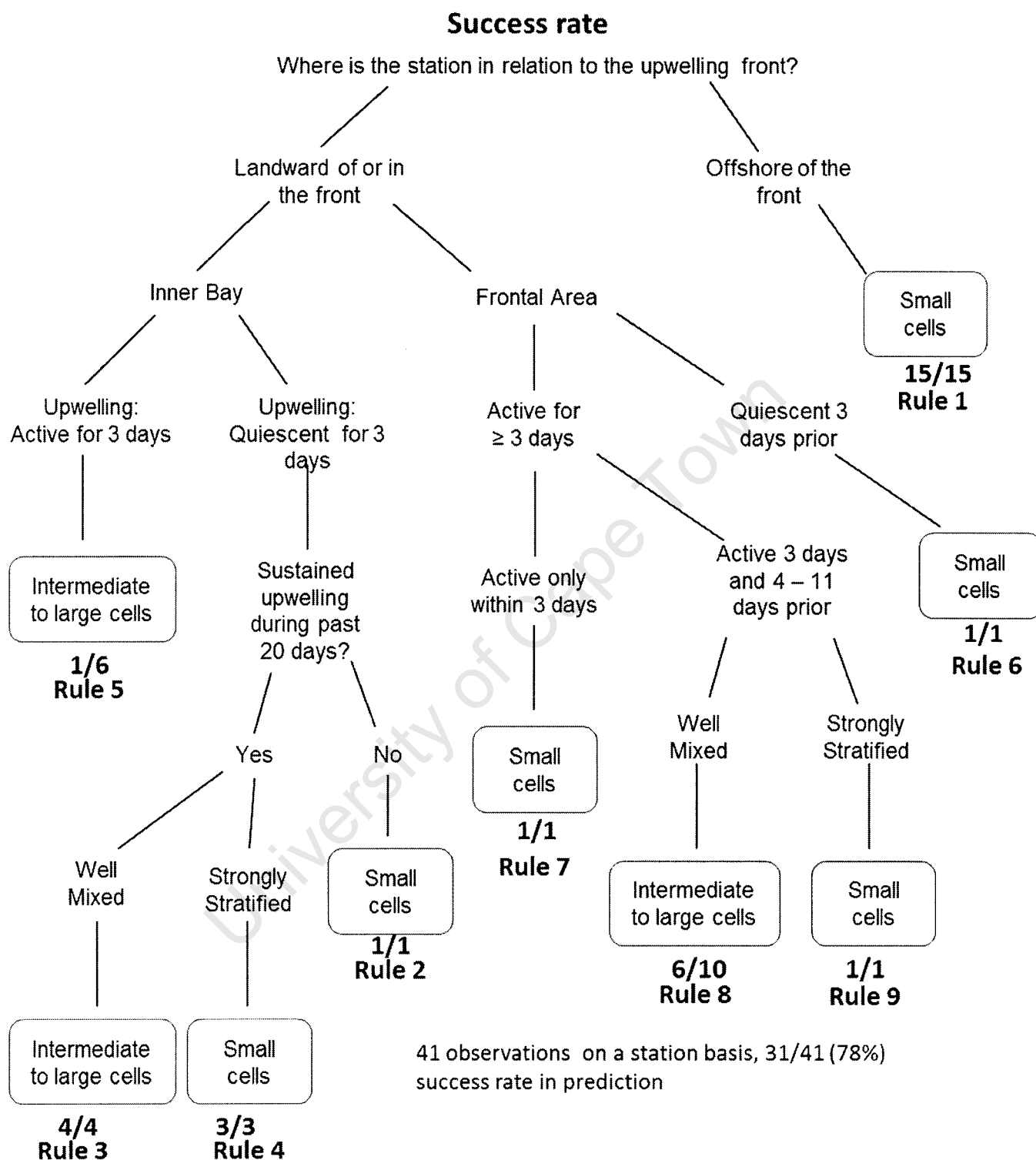
**Table 4** Summary of results for each cruise highlighting whether the observed particle size distribution conformed to what was expected from examining the state of upwelling and temperature profiles. The size classes used were small (< 10 µm), intermediate (10 – 30 µm) and large (> 30 µm), and the location of the maximum peak in volume is used. Upwelling (either quiescent or active) is displayed for 20, 10, five and one day prior to sampling. Particle spectra were either from the inner bay (stations 1 – 3), the frontal area (4 – 8) or offshore (9 – 12). The second last column refers to the location where deviation from the expected size distribution occurred. The last column refers to the percentage of locations for individual cruises which conformed to the expected size distribution. The rows “% success summer” and “% success winter” indicate percentage of samples for either inner bay, frontal area or offshore which conformed to the expected size distribution. See text for additional explanation of reasoning.

Season	Year	Month	Upwelling prior to cruise (days)				Observed size distribution			Deviation from expected distribution	Success percentage
			20	10	5	1	Inner bay (Stations 1 - 3)	Frontal area (Stations 4 - 8)	Offshore (Stations 9 - 12)		
Spring and Summer (October to March)	2000	December	a	a	a	a	S	I	S	expect larger cells at inner bay	67
	2002	December	a	a	q	q	S	S	S	expect larger cells in frontal area	67
	2004	December	a	a	a	a	S, I, L	I	S	dominance of small cells at station 1 not expected	67
	2001	January	a	q	a	a	S	I	S	expect larger cells at inner bay	67
	2001	February	a	a	a	a	S	S	S	expect larger cells at inner bay and frontal area	33
	2007	February	q	a	a	a	S	I	S	expect larger cells at inner bay	67
% success summer							17	67	100		
Autumn and Winter (April to September)	2001	April	a	a	a	q	I	S	S	expect larger cells in frontal area	67
	2001	June	q	q	q	q	S	S	S	-	100
	2002	June	a	q	q	a	I	S	S	-	100
	2003	June	a	a	a	q	L	I, L	S	-	100
	2006	June	q	a	a	q	S	S	S	expect larger cells at frontal area	67
	2006	August	a	a	a	a	S	S	S	expect larger cells at inner bay	67
	2000	September	a	q	q	q	S	I	S	-	100
	2004	September	a	q	q	a	L	S	S	expect larger cells at frontal area	67
	2006	September	q	q	q	a	S, I	I	S	-	100
% success winter							89	67	100		

**Cell sizes:** small (S): < 10 µm ESD; intermediate (I): 10 - 30 µm ESD; large (L): > 30 µm ESD

**Upwelling:** active (a) and quiescent (q)





**Figure 6** Success rate of observed particle spectra conforming to the expected size distribution, based on the expert system used in this project. For each path of questioning (branch) followed the number of observations which matched the decisions (in rounded boxes) and the total observations of that path are given Branch numbers refer to corresponding rules in the expert system. Explanation for the decision tree provided above. See Appendix D and enclosed CD for details.

## **Discussion**

The size distribution of phytoplankton communities is strongly coupled with hydrographic control of the flow of nutrients and dynamics of the upper mixed layer. Rapid changes of phytoplankton community composition and size structure occur during the development of upwelling and distinct phytoplankton assemblages are associated with each phase of the upwelling cycle (Armstrong et al., 1987; Pitcher, 1988; Pitcher et al., 1991; Walker & Pitcher, 1991). Phytoplankton particle size spectra have been shown to reflect these changes during the upwelling cycle; wind reversal causes a change in phytoplankton community composition (Olivieri et al., 1985).

Observations of the surface particle spectra collected on the regular cruises of the SHBML and analysed by the Coulter Counter have revealed consistent patterns that are largely explained by the state of upwelling, but there are also several features of the particle spectra that are not explained by these data (table 4). Temperature data were used as an additional indication of the dynamics of the upper mixed layer. Active upwelling mixes the water column, eroding the thermocline and mixing nutrients and seed cells upwards. Relaxation of upwelling permits surface warming of the water column and stratification and nutrients are rapidly depleted as phytoplankton in the euphotic zone grows rapidly. In addition newly upwelled surface water in St. Helena Bay mixes with surrounding water soon after relaxation of upwelling, which may alter the dominant phytoplankton.

### **Particle spectra observations**

The weakening of winds in the winter months (April to September) resulted in weaker upwelling than in summer months. Wind-driven upwelling enhances primary production and chlorophyll *a* and SST satellite measurements and pigment analyses show the seasonal cycles of phytoplankton in the Southern Benguela at the class level (Barlow et al., 2005). However, there was no distinct seasonal signal displayed in the particle spectra, i.e. particle spectra from either winter or summer months could not be distinguished. By analysing the particle spectra in relation to the pulsed upwelling, the seasonal signal is aliased by localised short-term events (figure 3).

Although no seasonal signal was evident, observed particle spectra conformed to the expected size distribution, for the SHBML as a whole, 56% of winter samples whereas there was deviation from the expected size distribution in all of the summer months. Although, based on the expert system and on a station basis 78% of observations conformed to the expected size distribution. Results are as expected except for two

branches of the decision tree (mentioned below). Deviations from the expected size distribution were not related to the frequency of upwelling events prior to sampling.

Deviations from the expected size distribution from inner bay stations occurred during summer months for a situation of active upwelling for three or more days before the cruise where cells were smaller than expected (rule 5 of expert system; figure 6). The powerful upwelling during summer months could possibly have flushed large cells out of the bay at the surface. Huete-Ortega et al. (2010) found that at the peak of the upwelling event when upward vertical water velocities are the highest and strong turbulence exists and combined with an offshore dispersion of cells the accumulation of large cells is impeded. During the relaxation of upwelling, enhanced nutrient availability, water column stability and reduced dispersion allowed blooms of chain-forming diatoms to establish, which would be measured as large cells by the Coulter Counter. However, St Helena Bay does not experience much offshore loss as the water tends to follow a clockwise circulation in the Bay (Chapman and Bailey 1991). In addition the water stabilisation after upwelling in summer is very rapid, as solar radiation heats the cold, newly upwelled water mass as a thin layer of 5-10m thick, and nutrient depletion in the surface layer may be extremely rapid, allowing small cells to dominate when one would expect chain-forming diatoms. Alternatively seeding processes may be playing an important role.

Deviation from the expected size distribution from frontal area stations occurred in both summer and winter months. Again, the prevalence of small cells was more than expected in the frontal area. Deviations occurred in the frontal area when multiple upwelling events preceded sampling within four to 11 days and waters were well-mixed (rule 8 of expert system; figure 6). Advection from further south (unmeasured buoyancy effect) and complex mixing and sinking in frontal waters may be responsible for such deviations.

Observed particle spectra conformed to the expected size distribution for all offshore stations (rule 1 of expert system; figure 6). Offshore of the upwelling front cells less than 10  $\mu\text{m}$  ESD dominated the particle spectra. Larger cells were also less prevalent offshore than inshore of the upwelling front. Beyond the front, warm stratified and nutrient-poor surface water, originating from the Agulhas Bank favours the dominance of small cells. Similarly, Armstrong et al. (1987) reported on particle spectra collected in St. Helena Bay from either side of the upwelling front. Particle spectra from oceanic water were relatively flat and large cells dominated at the landward side of the front and at the upwelling front. Particle spectra collected from the outer four stations would have limited use as an ecosystem indicator because small cells dominated these particle

spectra most of the time, regardless of upwelling condition. Future sampling should therefore be focussed on frontal area and inner bay stations.

Small cells dominated waters on most occasions and were more prevalent than expected. However, on many of cruises large cells were also prevalent albeit at a lower concentration (April 2001; June 2001, 2002, 2003, 2006; September 2004; December 2004). Upwelling increased the prevalence of large cells in the inner bay and frontal area as expected by size-based theory. Small cells are present at background levels and contribution by larger cells increases as nutrient influxes (Sprules & Munawar, 1986; Ahrens & Peters, 1991; Chisholm, 1992; Arin, 2002; Cullen et al., 2002).

The deviations from the expected size distribution of particle spectra could have occurred for two reasons. Firstly, the ability to predict the expected size distribution from upwelling and temperature data affects whether the observed size distribution conforms to what is expected from size-based theory. Included in this is the ability to characterise upwelling features relevant to phytoplankton. Two methods of calculating positive continuous divergence were used in this study. Firstly, upwelling events were defined as uninterrupted positive divergence and secondly, uninterrupted divergence with wind speeds that did not decrease more than  $5\text{m.s}^{-1}$  per day. The overall interpretation of results was not sensitive to these categories of divergence. The insensitivity suggests that the upwelling index used in this study did not capture smaller-scale upwelling processes relevant to phytoplankton-sized cells, e.g. turbulent mixing, cell physiology and nutrient enrichment processes, which should be regarded in future work.

Secondly, inconsistencies arise as a result of the inherent nature of particle spectra, which represent a complex assemblage of detritus, phytoplankton, zooplankton, other living particles and the interaction between these components. As low as 40% of the total particle volume can be linked with living phytoplankton expressed as chlorophyll *a* (Table 2). The Coulter Counter is not able to distinguish between phytoplankton cells and detritus or between heterotrophs and autotrophs. The presence of detritus in newly upwelled water varies from inconsequential to composing the majority of water samples (Armstrong et al., 1987). The effect of grazing is more likely to alter phytoplankton particle spectra in summer months. However, top-down control through zooplankton grazing is unlikely to be a factor because the St. Helena Bay phytoplankton community is not shaped by grazing (Pers. Comm. L. Hutchings). Particle spectra could be of greater value, in these circumstances, if the 'phytoplankton signal' could be isolated from the detrital signal.

Additionally, individual cruises represent localised conditions and particle spectra may represent the biology of multiple upwelling events and mixing of different aged water

masses after upwelling. Sequential changes in the phytoplankton population caused by advection of nearby water and local reseeded and in combination with other factors sometimes produced unexpected particle spectra. The patterns of species succession affected by both the frequency and intensity of upwelling. Autochthonous populations may be continually translocated by intense upwelling (Pitcher et al., 1991). This is more likely in the frontal area, but there are also periodic incursions of different water masses in the bay (Pitcher et al., 1991). The source water of seed stock is affected by the strength of upwelling. Walker and Peterson (1991) found that diatom-dominated water mass originated during strong upwelling from a deep saline layer containing seed stock of diatom and dinoflagellate resting stages, which have high rates of sinking and accumulate on the sea bed. Seed stock originating from a shallower layer is advected to the surface when upwelling weakens. The shallower layer was found only to contain microflagellates (Walker and Peterson 1991). Prediction of the expected size distribution by size-based theory could possibly be hampered because physical factors such as seeding or sinking may also be important in determining which phytoplankton group dominates a particular water mass (Walker and Peterson, 1991).

Phytoplankton particle spectra could not consistently indicate the state of the phytoplankton in St. Helena Bay for the frontal area, and without a valid explanation for the observed deviations particle spectra could not be used reliably in these circumstances as a basis for an ecosystem indicator. However, even though the observed particle spectra did not indicate the theoretical state of the phytoplankton in the inner bay for summer, the explanation provided above reasons that particle spectra have the potential to be used in the inner bay. Particle spectra did indicate the state of the phytoplankton in St. Helena Bay for the inner bay in 89% of winter months covering all three size ranges. Phytoplankton particle spectra were also used to confirm phytoplankton community state, such as the dominance of small cells in warm, stratified water and an increase in prevalence of large cells with nutrient influx.

### **Food web structure and function**

A large fraction of phytoplankton production flows through the pelagic food chain (Fenchel, 1988). The transfer of energy to higher trophic levels varies with algal species composition. The dominant trophic pathways and transfer efficiency also vary with phytoplankton cell size (Cloern & Dufford, 2005). The microbial loop dominates in conditions where very small cells dominate the base of the food chain, as is the case in oligotrophic waters. The import of nutrients favours the dominance of large-celled phytoplankton communities and under these conditions a greater proportion of primary production is channelled to larger organisms (Fenchel, 1988). Zooplankton production and fecundity is linked to the quality of phytoplankton available in terms of size, species composition and nutritional state (Morey-Gaines, 1979; Checkley Jr, 1980a; 1980b;

Cahoon, 1981; Price et al., 1983; Runge, 1984; Price & Paffenhofer, 1983; 1985; Peterson & Bellantoni, 1987; Kiorboe, 1989; Walker & Peterson, 1991; Mitchell-Innes & Pitcher, 1992).

The feeding behaviour of pelagic fish, such as anchovy and sardine, is in turn mediated by the size of plankton particles (van der Lingen et al., 2006). Sardine is highly efficient at filter feeding over the size range 400 to 1200  $\mu\text{m}$  ESD. They are less efficient at retaining particles less than 400  $\mu\text{m}$  ESD but, can retain cells down to 10 $\mu\text{m}$  ESD in size, enabling sardines to feed directly on micro-phytoplankton. Clearance increases with particle size and size selectivity for large particles, removed during particulate feeding. Particulate feeding is the primary feeding mode for anchovy. For anchovy, the switch from filter feeding to particulate feeding occurs at particles 700  $\mu\text{m}$  in size (James & Findlay, 1989). The minimum size trapped by Anchovy during filtering is 200 to 250  $\mu\text{m}$  ESD which makes a large portion of phytoplankton unavailable to anchovy. Anchovy select for the largest particles available, generally larger than particles ingested by sardine. The switch in dominance of abundance between small pelagic fish species may therefore be trophodynamically mediated (van der Lingen et al., 2006).

The likelihood of small-, intermediate- or large-size phytoplankton can be used to describe the structure and function of the pelagic food web. For example, during persistent downwelling conditions small phytoplankton dominates the community, small zooplankton consume these phytoplankton and sardine is likely to have feeding conditions conducive to good recruitment. During sustained powerful upwelling larger-celled phytoplankton are expected to dominate in the bay which would favour the growth of large-celled zooplankton and successful recruitment and growth for anchovy.

Monitoring pelagic ecosystems using plankton indicators has been suggested because plankton is a major source of energy for fish in at least some stage of their life. Plankton is also the first level in the pelagic food web to respond to hydroclimatic forcing. Hydroclimatic variability effects plankton and ultimately has a strong impact on the entire ecosystem (Beaugrand, 2005). Indicators are only valuable if the data used to formulate them is collected easily and reliably (Shin et al., 2005). The benefits of phytoplankton particle spectra are that data are easy to work with, there are few steps in processing the data, the output is communicable and understanding of the data is fairly intuitive. Concentration and size are concepts non-scientific stakeholders can understand.

Particle spectra analysed by the Coulter Counter are easier to collect than taxonomic samples, but their reliability is dependent on the assemblage of detritus, autotrophs and

non-phytoplankton cells present. In this study a significant portion of total particle volume can be linked with phytoplankton abundance, expressed as chlorophyll *a*.

The results indicate that the use of particle spectra in St. Helena Bay appears to be limited to the inner bay in winter months. This is nevertheless significant, because this is the period when fish recruits are present in the bay to feed. The next step in development of an ecosystem indicator using particle spectra collected during winter from the inner bay is to link phytoplankton volume of cells larger than 10  $\mu\text{m}$  ESD to zooplankton concentration in an index of productivity for zooplankton production and relate it to biomass and condition of recruits. Whereas zooplankton data are available from the regular monthly sampling on the SHBML during the period covered here (2000–2007), high-resolution data on fish abundance from acoustics need to be scrutinised. However, both were beyond the scope of the present project.

University of Cape Town

## Chapter 3: Concluding remarks

This last chapter concludes the research, discusses possible sources of error in the project methods and outlines work that warrants future attention.

### *Critique of methods*

#### **Wind data, cumulative divergence and defining upwelling**

Deviations of observed particle spectra from expected size distributions could have been caused by the presence of non-phytoplankton cells, but may have also been, in part, due to the way in which the prevailing upwelling conditions were characterised. A cumulative wind-driven upwelling index was chosen to indicate upwelling conditions because wind events have been highlighted as an important hydrographic factor controlling the distribution and composition of phytoplankton communities. Upwelling also has a cumulative effect on ecosystem productivity (Armstrong et al., 1987; Pitcher, 1988; Bograd et al., 2009).

There are numerous other upwelling indices, but all less suitable for the purposes of this study than the cumulative upwelling index. In the Southern Benguela upwelling has been defined by alongshore wind speed greater than  $5 \text{ m.s}^{-1}$  (Shannon & Pillar, 1986) and also by temperature differentials between inshore and offshore water (Weeks et al., 2008). Suites of physical and chemical descriptors are often used to describe the activity of upwelling processes (Pitcher, 1988). Carr and Kearns (2003) reported that upwelled Benguela current water was between  $12 - 18 ^\circ\text{C}$  and between 34.9 and 35.3 psu, however this may be too coarse a scale for the processes of interest here.

The insensitivity of the results to the manner of defining upwelling events leads one to believe that the method used in this study does not capture smaller scale physical process relevant to phytoplankton growth and decay. The focus was on nutrient enrichment processes and less so on turbulent mixing processes. A descriptor of the turbulent mixing may be as important as an index of upwelling in predicting the phytoplankton size structure dominant at any given time. Walker and Peterson (1991) suggest that physical factors such as seeding or sinking may be as important as nutrient enrichment from upwelling in determining which phytoplankton group dominates a particular water mass. A recommendation for further study would be further characterisation/ description of mixing events and stratification using available CTD data.

Regarding the wind data, re-analysis winds were used because the dataset was the best available for the project, reliable and without gaps. The spatial resolution of re-



analysis winds is  $2.5^\circ$  instead of  $0.5^\circ$  offered by QuikSCAT scatterometer winds. It is possible that wind events on a smaller scale are more relevant to phytoplankton processes. The use of an upwelling index from two different data sources could possibly describe the full complexity of the phenomenon (Perez-Brunius et al., 2007). Further research into alternative sources of wind data (local records, scatterometer data, etc.) could have been used to ascertain the most accurate and relevant wind data source and formulate an upwelling index relevant for the requirements of the study. Sets of wind measurements made available more recently should be scrutinised in terms of their usefulness. This was beyond the scope of this minor dissertation.

### **Particle spectra analyses**

The principal limitation of particle spectra analysed by the Coulter Counter is the unidentifiable portion contributed by detritus and autotrophic cells. Separation of particle spectra into algal and detrital components using numerical methods is possible (Bernard, 2005). One can assume that the detrital component follows a Junge-type distribution (a power law function), and hence subtract this portion from the total measured size distribution (Bernard, 2005). However, detrital components have also been included in size structure analyses because they form part of the trophic transfer in the pelagic food web (Roy et al., 2000).

Alternate methods of counting and sizing phytoplankton particles are available. Flow cytometry has been used to enumerate phytoplankton cells with high precision, rapidly and aboard ships. It is possible to discriminate phytoplankton cells from bacteria, suspended sediment and detritus (Yentsch & Yentsch, 2008). Light scattering properties and fluorescence can be simultaneously measured with flow cytometry (Shalapyonok et al., 2001).

A dual analysis with surface particle spectra and chlorophyll a max spectra investigating which conforms better to the expected size distribution could have been done. The total volume of each size class reported at different sampling depths would form a separate analysis in a future study. Such an investigation could potentially aid in determining whether a composite of sampling depths would better describe the phytoplankton community in St Helena Bay.

Identifying the differences among the particle spectra could have been augmented with a quantitative approach. Polydisperse particle distributions are described by the effective diameter, an average volume to surface area ratio. The effective diameter describes the average cell size so includes data of dominant cell sizes but also those prevalent at a lower concentration. Cumulative volume plots indicate which cell size fraction adds the largest proportion of volume to the particle spectra, i.e. such plots may

indicate whether small, intermediate or large cells contribute the most volume to the sample. Curves fitted to cumulative volume plots can be tested by statistics. Approaches that quantify the phytoplankton population despite non-phytoplankton cells would be valuable in further analyses of particle spectra.

Errors can be expected with Multisizer data; associated with particle size and cell volume parameters. Co-incidence of small cells occurs at very high concentrations and results in an underestimation of particle volume. Dilution of samples reduces coincidence and the coincidence factor can be determined by comparison of diluted and undiluted samples. Coincidence of samples from cruises used in this study was low and samples were not diluted (Pers. Comm. L. Hutchings). It is good practice to analyse replicate water samples for phytoplankton particle spectra. However, observed deviation among samples at the time of collection was low. Hence, no replicates were analysed. Additionally, on-board analysis is time consuming (Pers. Comm. L. Hutchings). Retrospectively, it is not possible to estimate the measurement error in the data used in this study. Measurement error can be estimated in future sampling. Other potential measurement errors are discussed in chapter One, with respect to the limitations of the Coulter Counter measuring equipment.

### ***Future work***

Research regarding description or quantification of the non-phytoplankton component of the particle size spectra is necessary. Accurate characterisation of the physical regime relevant to phytoplankton particle spectra would aid further research of particle spectra as an indication of the state of the phytoplankton community. The mechanisms whereby seeding of localised upwelled water masses occur would help to reduce the uncertainty inherent in particle spectra data, particularly in summer. The reasons why small cells are so much more frequent than normal in St. Helena Bay also needs further attention. Following the suggested research, the next step would be to investigate whether the phytoplankton particle spectra can be linked to zooplankton observations and hence formulated into a meaningful indicator of the structure of the planktonic food web. Zooplankton abundance data collected on monthly SHBML cruises are readily available and should be used in combination with available fish abundance data to provide composite indicators.

## References

- Ahrens, M. & Peters, R. (1991) Patterns and limitations in limnoplankton size spectra. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1967-1978.
- Alcaraz, M., Saiz, E., Marrase, C. & Vaque, D. (1988) Effects of turbulence on the development of phytoplankton biomass and copepod populations in marine microcosms. *Marine Ecology Progress Series*, **49**, 117-125.
- Ambler, J.W. (1986) Effect of Food Quantity and Quality on Egg Production of *Acartiatonsa Dana* from East Lagoon, Galveston, Texas. *Estuarine, Coastal and Shelf Science*, **23**, 183-196.
- Arin, L. (2002) Phytoplankton size distribution and growth rates in the Alboran Sea (SW Mediterranean): short term variability related to mesoscale hydrodynamics. *Journal of Plankton Research*, **24**, 1019-1033.
- Andrews, W.R.H. & Hutchings, L. (1980) Upwelling in the southern Benguela Current. *Progress in Oceanography*, **9**, 81pp.
- Armstrong, D., Mitchell-Innes, B., Verheye-Dua, F., Waldron, H.N. & Hutchings, L. (1987) Physical and biological features across an upwelling front in the southern Benguela. *South African Journal of Marine Science*, **5**, 171-190.
- Armstrong, D., Verheye, H. & Kemp, A.D. (1991) Short-term variability during an anchor station study in the southern Benguela upwelling system: Fecundity estimates of the dominant copepod, *Calanoidescarinatus*. *Progress in Oceanography*, **28**, 167-188.
- Azam, F., Fenchel, T., Field, J., Gray, J., Meyer-Reil, L. & Thingstad, F. (1983) The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, **10**, 257-263.
- Barlow, R., Louw, D., Balarin, M. & Alheit, J. (2006) Pigment signatures of phytoplankton composition in the northern Benguela ecosystem during spring. *African Journal of Marine Science*, **3**, 479-491.
- Barlow, R., Sessions, H., Balarin, M., Weeks, S., Whittle, C. & Hutchings, L. (2005) Seasonal variation in phytoplankton in the southern Benguela: pigment indices and ocean colour. *African Journal of Marine Science*, **27**, 275-288.
- Bakun, A. (1975) Daily and weekly upwelling indices, west coast of North America, 1967-1973. U.S. Department of Commerce, NOAA Technical Report NMFS SSRF-693.p. 114.

- Beaugrand, G. (2005) Monitoring pelagic ecosystems using plankton indicators. *ICES Journal of Marine Science*, **62**, 333-338.
- Beaulieu, S.E., Mullin, M.M., Tang, V.T., Pyne, S.M., King, L. & Twining, B.S. (1999) Using an optical plankton counter to determine the size distributions of preserved zooplankton samples. *Journal of Plankton Research*, **21**, 1939-1956.
- Beers, J. & Reid, F. (1982) Seasonal abundance of the microplankton population in the North Pacific central gyre. *Deep Sea Research Part A*, **29**, 227-245.
- Berman, T. & Shteinman, B. (1998) Phytoplankton development and turbulent mixing in Lake Kinneret (1992–1996). *Journal of plankton research*, **20**, 709.
- Bernard, S. (2005) The Bio-Optical Detection of Harmful Algal Blooms. PHD thesis, Oceanography department, University of Cape Town. p188.
- Bianchi, G. (2000) Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science*, **57**, 558-571.
- Boden, B. & Day, J. (1949) Some marine plankton diatoms from the west coast of South Africa. *Transactions of the Royal Society of South Africa*, **32**, 321-434.
- Bograd, S.J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W.J. & Schwing, F.B. (2009) Phenology of coastal upwelling in the California Current. *Geophysical Research Letters*, **36**, 1-5.
- Borgmann, U. & Whittle, D. (1983) Particle-Size-Conversion Efficiency and Contaminant Concentrations in Lake Ontario Biota. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 328-336.
- Boyd, C.M. (1976) Selection of particle sizes by filter-feeding copepods: A plea for reason. *Limnology and Oceanography*, **21**, 175–180.
- Brey, T. (1990) Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. *Archive of fishery and marine research*, **32**, 329-343.
- Brown, P. (1984) Primary production at two contrasting nearshore sites in the southern Benguela upwelling region, 1977 - 1979. *South African Journal of Marine Science*, **2**, 205-215.
- Brown, P. & Hutchings, L. (1985) Phytoplankton distribution and dynamics in the southern Benguela Current. *International Symposium on Upwelling off West Africa, Inst. Inv. Pesq., Barcelona*. pp. 319-344.

- Brown, P.C. & Hutchings, L. (1987) The development and decline of phytoplankton blooms in the southern Benguela upwelling system. 2. Nutrient relationships. *South African Journal of Marine Science*, **5**, 393-409.
- Brown, S.L. & Landry, M.R. (2001) Microbial community structure and biomass in surface waters during a Polar Front summer bloom along 170 degrees W. *Deep Sea Research Part II: Topical Studies in Oceanography*, **48**, 4039-4058.
- Brown, J., Gillooly, J., Allen, A., Savage, V. & West, G. (2004) A metabolic theory of ecology. *Ecology*, **85**, 1771-1789.
- Brussaard, C., Riegman, R., Noordeloos, A., Cadée, G., Witte, H., Kop, A., Nieuwland, G., Duyl, F. Van & Bak, R. (1995) Effects of grazing, sedimentation and phytoplankton cell lysis on the structure of a coastal pelagic food web. *Marine ecology progress series*, **123**, 259-271.
- Cahoon, L. (1981) Reproductive response of *Acartiatonsa* to variations in food ration and quality. *Deep Sea Research Part A. Oceanographic Research*, **28**, 1215-1221.
- Carr, M.E. (2001) Estimation of potential productivity in Eastern Boundary Currents using remote sensing. *Deep Sea Research Part II: Topical Studies in Oceanography*, **49**, 59-80.
- Cavender-Bares, K.K., Rinaldo, A. & Chrisholm, S. (2001) Microbial size spectra from natural and nutrient enriched ecosystems. *Limnology and Oceanography*, **46**, 778-789.
- Chapman, P. & Bailey, G.W. (1991). Short-term variability during an anchor station study in the southern Benguela upwelling system: Introduction. *Progress in Oceanography*, **28**, 1-7.
- Checkley Jr., D.M. (1980a) California Food limitation of egg production by a marine, planktonic copepod in the sea off southern California. *Limnology and Oceanography*, **25**, 991-998.
- Checkley Jr., D.M. (1980b) The Egg Production of a Marine Planktonic Copepod in Relation to its Food Supply: Laboratory Studies. *Limnology and Oceanography*, **25**, 430-446.
- Chisholm, S.W. (1992) Phytoplankton size. *Primary Productivity and Biogeochemical Cycles in the Sea*. (eds. P. Falkowski & A. Woodhead), pp. 213-237. Plenum Press, New York.
- Cloern, J.E. & Dufford, R. (2005) Phytoplankton community ecology: principles applied in San Francisco Bay. *Marine Ecology Progress Series*, **285**, 11-28.

- Coetzee, J.C., Merkle, D., Hutchings, L., Lingen, C. Van der, Berg, M. van den & Durholtz, M.D. (2010) The 2005 KwaZulu-Natal sardine run survey sheds new light on the ecology of small pelagic fish off the east coast of South Africa. *African Journal of Marine Science*, **32**, 337-360.
- Cottingham, K.L. (1999) Nutrients and Zooplankton as Multiple Stressors of Phytoplankton Communities: Evidence from Size Structure. *Limnology and Oceanography*, **44**, 810-827.
- Crawford, R. (1980) Seasonal patterns in South Africa's Western Cape purse-seine fishery. *Journal of Fish Biology*, **16**, 649-664.
- Cullen, J., Franks, P., Karl, D.M. & Longhurst, A.R. (2002) Physical influences on marine ecosystem dynamics. *The Sea*. (eds A. Robinson, J. McCarthy & B. Rothschild), pp. 297-336. John Wiley & Sons, New York.
- Cushing, D.H. (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. *Journal of Plankton Research*, **11**, 1-13.
- Cózar, A., Garcia, C. & Gálvez, J.A. (2003) Analysis of plankton size spectra irregularities in two subtropical shallow lakes (Esteros del Iberá, Argentina). *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 411-420.
- deJager, B. (1954) Plankton studies in and around St. Helena Bay, 1950-51. *Division of Fisheries Investigational Report*, **17**, 1-26.
- Denney, N., Jennings, S. & Reynolds, J. (2002) Life-history correlates of maximum population growth rates in marine fishes. *Proceedings of the Royal Society of London Biological Sciences*, **269**, 2229-2237.
- Dickie, L., Kerr, S. & Boudreau, P. (1987) Size-dependent processes underlying regularities in ecosystem structure. *Ecological Monographs*, **57**, 233-250.
- Duarte, C., Agustí, S. & Agawin, N.S.R. (2000) Response of a Mediterranean phytoplankton community to increased nutrient inputs: a mesocosm experiment. *Marine Ecology Progress Series*, **195**, 61-70.
- Dugdale, R. & Wilkerson, F. (1992) Nutrient limitation of new production in the sea. *Primary Productivity and Biogeochemical Cycles in the Sea*. (eds P. Falkowski & A. Woodhead), pp. 107-122. Plenum Press, New York.
- Echevarría, F., Carillo, P., Jimenez, F., Sanchez-Castillo, P., Cruz-Pizarro, L. & Rodriguez, J. (1990) The size-abundance distribution and taxonomic composition of plankton in an oligotrophic, high mountain lake (La Caldera, Sierra Nevada, Spain). *Journal of Plankton Research*, **12**, 415-422.

- Elton, C. (1927) *Animal Ecology*. pp. 67-94. Sidgwick and Jackson, London.
- Eppeley, R.W. & Peterson, B. (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, **282**, 677-680.
- FAO.(2003) *FAO Technical guidelines for responsible fisheries*. Rome.
- FAO. (2005) *Putting into practice the ecosystem approach to fisheries*. Rome.
- FAO. (2004) *The state of world fisheries and aquaculture*. Rome.
- Falkowski, P., Scholes, R., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Hogberg, P., Linder, S., Mackenzie, F., Moore III, B., Pedersen, T., Rosenthal, Y., Seitzinger, S., Smetacek, V. & Steffen, W. (2000) The Global Carbon Cycle: A Test of Our Knowledge of Earth as a System. *Science*, **290**, 291-296.
- Fenchel, T. (1974) Intrinsic rate of natural increase: the relationship with body size. *Oecologia*, **14**, 317–326.
- Fenchel, T. (1988) Marine Plankton Food Chains. *Annual Review of Ecology and Systematics*, **19**, 19-38.
- Fry, B. & Quinones, R. (1994) Biomass spectra and stable isotope indicators of trophic level in zooplankton of the northwest Atlantic. *Marine ecology progress series*. *Oldendorf*, **112**, 201–204.
- Fuchs, H. & Franks, P. (2010) Plankton community properties determined by nutrients and size-selective feeding. *Marine Ecology Progress Series*, **413**, 1-15.
- Gaedke, U. (1993) Ecosystem analysis based on biomass size distributions: a case study of a plankton community in a large lake. *Limnology and oceanography*, **38**, 112-127.
- Gaedke, U. (1992a) Identifying ecosystem properties: a case study using plankton biomass size distributions. *Ecological Modelling*, **63**, 277-298.
- Gaedke, U. (1992b) The size distribution of plankton biomass in a large lake and its seasonal variability. *Limnology and Oceanography*, **37**, 1202–1220.
- Gaedke, U., Seifried, A. & Adrian, R. (2004) Biomass Size Spectra and Plankton Diversity in a Shallow Eutrophic Lake. *International Review of Hydrobiology*, **89**, 1-20.
- Gamble, A., Lloyd, R., Aiken, J., Johannsson, O. & Mills, E. (2006) Using zooplankton biomass size spectra to assess ecological change in a well-studied freshwater lake

- ecosystem: Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 2687-2699.
- Gasol, J., del Giorgio, P. & Duarte, C. (1997) Biomass distribution in marine planktonic communities. *Limnology and Oceanography*, **42**, 1353-1363.
- Gasol, J., Guerrero, R. & Pedros-Alio, C. (1991) Seasonal variations in size structure and procaryotic dominance in sulfurous Lake Ciso. *Limnology and oceanography*, **36**, 860-872.
- Goericke, R. (1998) Response of phytoplankton community structure and taxon-specific growth rates to seasonally varying physical forcing in the Sargasso Sea off Bermuda. *Limnology and Oceanography*, **43**, 921-935.
- Goldman, J.C. & McGillicuddy, D.J. (2003) Effect of large marine diatoms growing at low light on episodic new production. *Limnology and Oceanography*, **48**, 1176-1182.
- Griesbach, S. & Peters, R.H. (1982) An Allometric Model for Pesticide Bioaccumulation. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 727-735.
- Hamm, C.E., Merkel, R., Springer, O., Jurkojc, P., Maier, C., Prectel, K. & Smetacek, V. (2003) Architecture and material properties of diatom shells provide effective mechanical protection. *Nature*, **421**, 841-3.
- Hansson, L.-A., Bergman, E. & Cronberg, G. (1998) Size Structure and Succession in Phytoplankton Communities: The Impact of Interactions between Herbivory and Predation. *Oikos*, **81**, 337.
- Havens, K. (1998) Size structure and energetics in a plankton food web. *Oikos*, **81**, 346-358.
- Havens, K.E., East, T.L. & Beaver, J.R. (1996) Experimental studies of zooplankton-phytoplankton- nutrient interactions in a large subtropical lake (Lake Okeechobee, Florida, U.S.A.). *Freshwater Biology*, **36**, 579-597.
- Hobson, L. (1988) Paradox of the Phytoplankton - An Overview. *Biological Oceanography*, **6**, 493-504.
- Huete-Ortega, M., Marañón, E., Varela, M. & Bode, A. (2010) General patterns in the size scaling of phytoplankton abundance in coastal waters during a 10-year time series. *Journal of Plankton Research*, **32**, 1-14.
- Hutchings, L. & Nelson, G. (1985) The influence of environmental factors on the Cape pelagic fishery. *International Symposium on Upwelling off West Africa, Inst. Inv. Pesq., Barcelona*. pp. 523-540.



- Hutchings, L., Jarre, A., Lamont, T. & van der Berg, H. St. Helena Bay then and now: muted climate signals, large human impact. *Submitted to AJMS*, January 2012.
- Hutchings, L., Armstrong, D.A. Mitchell-Innes, B.A. (1986). The frontal zone in the southern Benguela current. *Marine interfaces ecohydrodynamics*(ed J.C.J Nihoul). pp. 67-94. Elsevier, Amsterdam.
- Hutchings, L., Holden, C. & Mitchell-Innes, B. (1984) Hydrological and Biological Shipboard Monitoring of Upwelling off the Cape Peninsula. *South African Journal of Science*, **80**, 83-89.
- Hutchings, L., Barlow, R., Brown, P. & Olivieri, E. (1983) Drogue drift and phytoplankton blooms in newly upwelled waters in the Southern Benguela current. *5th National Oceanographic Symposium. South African National Oceanographic Research. Rhodes University*. p. B16.
- Irwin, A., Finkel, Z., Schofield, O.M.E. & Falkowski, P. (2006) Scaling-up from nutrient physiology to the size-structure of phytoplankton communities. *Journal of Plankton Research*, **28**, 459-471.
- James, A.G. & Findlay, K.P. (1989) Effect of particle size and concentration on feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy *Engrauliscapensis*. *Marine Ecology Progress Series*, **51**, 275-294.
- Jennings, S. (2005) Size-based analysis of aquatic food webs. *Aquatic Food Webs*. (eds A. Belgrano, U. Scharler, J. Dunne & R. Ulanowicz), pp. 86-97. Oxford University Press, New York.
- Jennings, S., Pinnegar, J., Polunin, N.V.C. & Warr, K. (2002) Linking size-based and trophic analyses of benthic community structure. *Marine Ecology Progress Series*, **226**, 77-85.
- Johnson, N., Kotz, S. & Balakrishnan, N. (1994) *Continuous Univariate Distributions*. John Wiley & Sons.
- Kerr, S. (1979) Prey availability, metaphoresis, and the size structures of lake trout stocks. *Inv. Pesq.*, **43**, 187-198.
- Kerr, S. (1974) Theory of size distribution in ecological communities. *Journal of the Fisheries Research Board of Canada*, **31**, 1859-1862.
- Kerr, S. & Dickie, L. (2001) *The Biomass Spectrum: A predator-prey theory of aquatic production*. Columbia University Press, New York.

- Kjørboe, T. (1989) Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in a herbivorous copepod. *Marine Ecology Progress Series*, **55**, 229-234.
- Kistler, R., Collins, W., Saha, S., White, G., Woollen, J., Kalnay, E., Chelliah, M., Ebisuzaki, W., Kanamitsu, M., Kousky, V., Dool, H. van den, Jenne, R. & Fiorino, M. (2001) The NCEP–NCAR 50–Year Reanalysis: Monthly Means CD–ROM and Documentation. *Bulletin of the American Meteorological Society*, **82**, 247-267.
- Kjørboe, T. (1993) Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Advances in marine biology*, **29**, 1–61.
- Laws, E., Falkowski, P., Smith Jr., W., Ducklow, H. & McCarth, J. (2000) Temperature effects on export production in the open ocean. *Global Biogeochemical Cycles*, **14**, 1231-1246.
- Le Borgne, R., Feely, R.A. & Mackey, D.J. (2002) Carbon fluxes in the equatorial Pacific: a synthesis of the JGOFS programme. *Deep Sea Research Part II: Topical Studies in Oceanography*, **49**, 2425-2442.
- Legendre, L. & Le Fevre, J. (1991). From individual plankton cells to pelagic marine ecosystems and to global biogeochemical cycles. Particle analysis in oceanography, (ed S. Demers, S). pp. 26-299. Springer-Verlag, Berlin.
- Margalef, R. (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta*, **134**, 493-509.
- Marquet, P.A., Quiñones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M. & Rivadeneira, M. (2005) Scaling and power-laws in ecological systems. *The Journal of experimental biology*, **208**, 1749-69.
- Miller, D.C.M. & Field, J.G. (2002) Predicting anchovy recruitment in the Southern Benguela ecosystem: developing an expert system using classification trees. *South African Journal of Science*, **98**, 465-472.
- Mitchell-Innes, B. & Pitcher, G. (1992) Hydrographic parameters as indicators of the suitability of phytoplankton populations as food for herbivorous copepods. *South African Journal of Marine Science*, **12**, 355–365.
- Mitchell-Innes, B. & Walker, D. (1991) Short-term variability during an anchor station study in the southern Benguela upwelling system: Phytoplankton production and biomass in relation to specie changes. *Progress in Oceanography*, **28**, 65-89.
- Mitchell-Innes, B., Pitcher, G. & Probyn, T. (2000) Productivity of dinoflagellate blooms on the west coast of South Africa, as measured by natural fluorescence. *South African Journal of Marine Science*, **22**, 273–284.

- Moloney, C. & Field, J. (1985) Use of particle-size data to predict potential pelagic-fish yields of some southern African areas. *South African Journal of Marine Science*, **3**, 119–128.
- Moloney, C., Field, J. & Lucas, M. (1991) The size-based dynamics of plankton food webs. II. Simulations of three contrasting southern Benguela food webs. *Journal of Plankton Research*, **13**, 1039–1092.
- Morey-Gaines, G. (1979) The Ecological role of red tides in the Los Angeles-Long Beach Harbor Food Web. *Toxic Dinoflagellate Blooms*. (eds D. Taylor & H. Seliger), pp. 315–320. North Holland.
- Mulligan, H.F. & Kingsbury, J.M. (1968) Application of an Electronic Particle Counter in Analyzing Natural Populations of Phytoplankton. *Limnology and Oceanography*, **13**, 499–506.
- Mullin, M.M. (1965) Size fractionation of particulate organic carbon in the surface waters of the western Indian Ocean. *Limnology and Oceanography*, **10**, 459–462.
- Odum, H.T. (1971) *Environment, power and society*. Wiley, New York, NY. 331p
- Olivieri, E. (1983) Colonization, adaptations and temporal changes in diversity and biomass of a phytoplankton community in upwelled water off the Cape Peninsula, South Africa, in December 1979. *South African Journal of Marine Science*, **1**, 77–109.
- Olivieri, E. (1985) Feasibility of estimating phytoplankton size and biomass in fresh and preserved samples from the Benguela Current with a Coulter Counter. *South African Journal of Marine Science*, **3**, 99–110.
- Olivieri, E., Hutchings, L., Brown, P. & Barlow, R. (1985) The development of phytoplankton communities in terms of their particle size distribution, in newly upwelled waters of the southern Benguela Current. *International Symposium on Upwelling off West Africa, Inst. Inv. Pesq., Barcelona*. pp. 345–371.
- Perez-Brunius, P., Lopez, M., Pares-Sierra, A. & Pineda, J. (2007) Comparison of upwelling indices off Baja California derived from three different wind data sources. *CalCoFI Report*, **48**, 204–214.
- Peters, R. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Peterson, W.T. & Bellantoni, D.C. (1987) Relationships between water-column stratification, phytoplankton cell size and copepod fecundity in Long Island Sound and off central Chile. *South African Journal of Marine Science*, **5**, 411–421.

- Piontkovski, S., Williamson, R., Ignatyev, S., Boltachev, A. & Chesalin, M. (2003) Structural-functional relationships in the pelagic community of the eastern tropical Atlantic Ocean. *Journal of Plankton Research*, **25**, 1021-1034.
- Pitcher, G. (1988) Mesoscale heterogeneities of the phytoplankton distribution in St Helena Bay, South Africa, following an upwelling event. *South African Journal of Marine Science*, **7**, 9-23.
- Pitcher, G., Brown, P. & Mitchell-Innes, B. (1992) Spatio-temporal variability of phytoplankton in the southern Benguela upwelling system. *South African Journal of Marine Science*, **12**, 439-456.
- Pitcher, G., Walker, D., Mitchell-Innes, B. & Moloney, C. (1991) Short-term variability during an anchor station study in the southern Benguela upwelling system: Phytoplankton dynamics. *Progress in Oceanography*, **28**, 39-64.
- Platt, T. (1985) Structure of the Marine Ecosystem: Its Allometric Basis. *Ecosystem theory for biological oceanography*. pp. 55-64. Canadian Bulletin of Fisheries and Aquatic Sciences, 213.
- Platt, T. & Denman, K. (1977) Organisation in the pelagic ecosystem. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **30**, 575-581.
- Platt, T. & Denman, K. (1978) The structure of pelagic marine ecosystems. *Rapports et Procès-verbaux des Réunions. Conseil International pour l'Exploration de la Mer*, **173**, 60-65.
- Platt, T., Lewis, M.R. & Geider, R.J. (1984) Thermodynamics of the pelagic ecosystem: Elementary closure conditions for biological production in the open ocean. *Flows of energy and materials in marine ecosystems*. (ed M. Fasham), pp. 49-84. Plenum Publishing Corporation, New York.
- Platt, T., Mann, H. & Ulanowics, R. (1981) New explorations of ecosystem properties: a holistic view. *Mathematical models in biological oceanography*. pp. 72-79. Unesco Press.
- Poulet, S. (1977) Grazing of Marine Copepod Developmental Stages on Naturally Occurring Particles. *Journal of the Fisheries Research Board of Canada*, **34**, 2381-2387.
- Poulet, S. (1973) Grazing of *Pseudocalanus minutus* on naturally occurring particulate matter. *Limnology and Oceanography*, **18**, 564-573.
- Price, H.J. & Paffenhofer, G-A. (1985) Perception of food availability by Calanoid copepods. *Archiv für Hydrobiologie. Beihefte, Ergebnisse Limnologie*, **21**, 115-124.

- Price, H.J., Paffenhofer, G-A.&Strickler, J. (1983) Modes of cell capture in calanoid copepods. *Limnology and Oceanography*, **28**, 116-123.
- Probyn, T. (1985) Nitrogen uptake by size-fractionated phytoplankton populations in the southern Benguela upwelling system. *Marine Ecology Progress Series*, **22**, 249-258.
- Quadling, H. &Quadling, M. (1995) WinExp - A Small Expert System for Windows v2.11. University of Minneapolis, MN.
- Quiñones, R.A. (1994) A comment on the use of allometry in the study of pelagic ecosystem processes. *Scientia Marina (Barcelona)*, **58**, 11–16.
- Quiñones, R.A., Platt, T. & Rodríguez, J. (2003) Patterns of biomass-size spectra from oligotrophic waters of the Northwest Atlantic. *Progress in Oceanography*, **57**, 405-427.
- Reul, A. (2006) Control of microplankton size structure in contrasting water columns of the Celtic Sea. *Journal of Plankton Research*, **28**, 449-457.
- Rice, J. (2000) Evaluating fishery impacts using metrics of community structure. *ICES Journal of Marine Science*, **57**, 682-688.
- Rice, J. &Gislason, H. (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES Journal of Marine Science*, **53**, 1214-1225.
- Riley, G. A. (1963) Organic aggregates in seawater and the dynamics of their formation and utilization. *Limnology and Oceanography*, **8**, 372-381.
- Rinaldo, A., Maritan, A., Cavender-Bares, K.K. &Chrisholm, S. (2002) Cross-scale ecological dynamics and microbial size spectra in marine ecosystems. *Proceedings of The Royal Society of London Biological Sciences*, **269**, 2051-9.
- Rodríguez, J. & Mullin, M.M. (1986) Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. *Limnology and Oceanography*, **31**, 361-370.
- Rodríguez, J. (1994) Some comments on the size-based structural analysis of the pelagic ecosystem\*. *Scientia Marina*, **58**, 1-10.
- Rojo, C. & Rodríguez, J. (1994) Seasonal variability of phytoplankton size structure in a hypertrophic lake. *Journal of Plankton Research*, **16**, 317-335.

- Roy, C., Weeks, S., Rouault, M., Nelson, G., Barlow, R. & van der Lingen, C.D. (2001) Extreme oceanographic events recorded in the Southern Benguela during the 1999-2000 summer season. *South African Journal of Science*, **97**, 465-471.
- Runge, J. (1984) Egg production of the marine, planktonic copepod, *Calanus pacificus* Brodsky Laboratory observations. *Journal of Experimental Marine Biology and Ecology*, **74**, 53-66.
- San-Martin, E., Harris, R. & Irigoien, X. (2006) Latitudinal variation in plankton size spectra in the Atlantic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 1560-1572.
- Schartau, M., Landry, M.R. & Armstrong, R.A. (2010) Density estimation of plankton size spectra: a reanalysis of IronEx II data. *Journal of Plankton Research*, **32**, 1167-1184.
- Schwinghamer, P. (1981) Characteristic Size Distributions of Integral Benthic Communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1255-1263.
- Shalapyonok, A., Olson, R.J. & Shalapyonok, L.S. (2001) Arabian Sea phytoplankton during Southwest and Northeast Monsoons 1995: composition, size structure and biomass from individual cell properties measured by flow cytometry. *Deep Sea Research Part II: Topical Studies in Oceanography*, **48**, 1231-1261.
- Shannon, L. & Pillar, S. (1986) The Benguela Ecosystem: 3. Plankton. *Oceanography and Marine Biology: An annual review* 24. (ed M. Barnes), pp. 65-170. Aberdeen University Press.
- Shannon, L.V., Hutchings, L., Bailey, G.W. & Shelton, P.A. (1984) Spatial and temporal distribution of chlorophyll in southern African waters as deduced from ship and satellite measurements and their implications for pelagic fisheries. *South African Journal of Marine Science*, **2**, 109-130.
- Sheldon, R. (1979) Measurement of Phytoplankton Growth by Particle Counting. *Limnology and Oceanography*, **24**, 760-767.
- Sheldon, R. (1984) Phytoplankton growth rates in the tropical ocean. *Limnology and oceanography*, **29**, 1342-1346.
- Sheldon, R. & Kerr, S. (1972) The Population Density of Monsters in Loch Ness. *Limnology and Oceanography*, **17**, 796-798.
- Sheldon, R. & Parsons, T. (1967) A Continuous Size Spectrum for Particulate Matter in the Sea. *Journal of the Fisheries Research Board of Canada*, **24**, 909-915.

- Sheldon, R., Prakash, A. & Sutcliffe, WH, J. (1972) The size distribution of particles in the ocean. *Limnology and Oceanography*, **17**, 327-340.
- Sheldon, R., Sutcliffe, WH, J. & Paranjape, M. (1977) Structure of Pelagic Food Chain and Relationship Between Plankton and Fish Production. *Journal of the Fisheries Research Board of Canada*, **3**, 2344-2353.
- Shin, Y., Rochet, M., Jennings, S., Field, J. & Gislason, H. (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science*, **62**, 384-396.
- Sieburth, J.M. (1979) *Sea Microbes*. Oxford University Press, New York.
- Silvert, W. & Platt, T. (1978) Energy flux in the pelagic ecosystem: a time-dependent equation. *Limnology and Oceanography*, **23**, 813-816.
- Smayda, T.J. (1997) Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography*, **42**, 1137-1153.
- Smetacek, V. (1999) Diatoms and the ocean carbon cycle. *Protist*, **150**, 25-32.
- Sprules, W.G. & Goyke, A.P. (1994) Size-Based Structure and Production in the Pelagia of Lakes Ontario and Michigan. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2603-2311.
- Sprules, W.G. & Knoechel, R. (1984) Lake Ecosystem Dynamics Based on Functional Representations of Trophic Components. *Trophic Interactions within Aquatic Ecosystems*. (eds D. Meyers & J. Strickler), pp. 383-403. Westview Press, Boulder, CO.
- Sprules, W. & Munawar, M. (1986) Plankton Size Spectra in Relation to Ecosystem Productivity, Size, and Perturbation. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1789-1794.
- Sprules, W., Brandt, S., Stewart, D., Munawar, M., Jin, E. & Love, J. (1991) Biomass size spectrum of the Lake Michigan pelagic food web. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 105-115.
- Sprules, W., Casselman, J. & Shuter, B. (1983) Size Distribution of Pelagic Particles in Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1761-1769.
- Starfield, A.M. & Bleloch, A.H. (1983) Expert systems: an approach to problems in ecological management that are difficult to quantify. *Journal of Environmental Management*, **16**, 261-268.

- Steele, J.H. & Frost, B.W. (1977) The Structure of Plankton Communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **280**, 485-534.
- Thiebaut, M. & Dickie, L. (1992) Models of Aquatic Biomass Size Spectra and the Common Structure of their Solutions. *Journal of Theoretical Biology*, **159**, 147-161.
- Thomann, R.V. (1979) An analysis of PCB in lake Ontario using a size-dependent food chain model. *Perspectives on Ecosystem Modelling*. (eds D. Scavia & A. Robertson), pp. 293-320. Ann Arbor Science Publishers, Michigan.
- Thomann, R.V. (1981) Equilibrium Model of Fate of Microcontaminants in Diverse Aquatic Food Chains. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 280-296.
- Tittel, J., Zippel, B., Geller, W. & Seeger, J. (1998) Relationships between plankton community structure and plankton size distribution in lakes of northern Germany. *Limnology and Oceanography*, **43**, 1119-1132.
- Tremblay, J.-E., Legendre, L. & Theriault, J.-C. (1997) Size-differential Effects of Vertical Stability on the Biomass and Production of Phytoplankton in a Large Estuarine System. *Estuarine, Coastal and Shelf Science*, **45**, 415-431.
- Vanaverbeke, J., Steyaert, M., Vanreusel, A. & Vincx, M. (2003) Nematode biomass spectra as descriptors of functional changes due to human and natural impact. *Marine Ecology Progress Series*, **249**, 157-170.
- van der Lingen, C., Hutchings, L. & Field, J. (2006) Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science*, **3**, 465-477.
- Vezina, A.F. (1986) Body size and mass flow in freshwater plankton: models and tests. *Journal of Plankton Research*, **8**, 939-956.
- Vidondo, B., Prairie, Y.T., Blanco, J. & Duarte, C. (1997) Some aspects of the analysis of size spectra in aquatic ecology. *Limnology and Oceanography*, **42**, 184-192.
- Waite, A.M., Thompson, P.A. & Harrison, P.J. (1992) Does energy control the sinking rates of marine diatoms? *Limnology and Oceanography*, **37**, 468-477.
- Walker, D. & Peterson, W. (1991) Relationships between hydrography, phytoplankton production, biomass, cell size and species composition, and copepod production in the southern Benguela upwelling system in April 1988. *South African Journal of Marine Science*, **11**, 289-305.



- Walker, D. & Pitcher, G. (1991) The dynamics of phytoplankton populations, including a red-tide bloom, during a quiescent period in St Helena Bay, South Africa. *South African Journal of Marine Science*, **10**, 61-70.
- White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between body size and abundance in ecology. *Trends in ecology & evolution*, **22**, 323-30.
- Witek, Z. & Krajewska-Soltys, A. (1989) Some examples of the epipelagic plankton size structure in high latitude oceans. *Journal of Plankton Research*, **11**, 1143-1155.
- Yentsch, C.S. & Yentsch, C.M. (2008) Single cell analysis in biological oceanography and its evolutionary implications. *Journal of Plankton Research*, **30**, 107-117.
- Zwanenburg, K. (2000) The effects of fishing on demersal fish communities of the Scotian Shelf. *ICES Journal of Marine Science*, **57**, 503-509.

University of Cape Town

## Appendix A

### **Wind data and cumulative divergence**

#### **Wind speed parallel to coast**

$$WW = V\cos(180^\circ - \theta) - U\sin(180^\circ - \theta)$$

V = South-North wind speed in  $m.s^{-1}$

U = West-East wind speed in  $m.s^{-1}$

$\Theta$  = coastal angle (as defined by NOAA as the angle the landward side of the coastline makes with a vector pointing north and taken as  $147^\circ$  for Cape Columbine)

**Drag coefficient (a function of wind speed, Large and Pond, 1981; Trenberth, 1990)**

$$C_d = \begin{cases} 0.00218 ; |WW| \leq 1m.s^{-1} \\ 0.001 \times \left(0.62 + \frac{1.56}{|WW|}\right) ; 1m.s^{-1} < |WW| \leq 3m.s^{-1} \\ 0.00114 ; 3m.s^{-1} < |WW| \leq 10m.s^{-1} \\ 0.001 \times (0.49 + 0.065 \times |WW|) ; |WW| > 10m.s^{-1} \end{cases}$$

#### **Wind stress ( $kg.m^{-1}.s^{-2}$ )**

$$\tau = C_d \rho_a V_y^2$$

$\rho_a$  is the density of air (taken as  $1.22521 kg.m^{-3}$ )

$V_y$  the alongshore wind component in  $m.s^{-1}$

#### **Ekman divergence ( $m^3.s^{-1}$ per 100m of coast)**

$$S = \frac{\tau}{\rho_w f}$$

$\rho_w$  = the density of the upper water layer;  $1026.17 kg.m^{-3}$

$f$  = Coriolis parameter

#### **Coriolis parameter**

$$f = 2\Omega \sin \varphi$$

$\Omega$  = angular velocity taken as  $7.29212\text{E-}05 \text{ rad.s}^{-1}$

$\varphi$  = latitude taken as  $32.83^\circ$

Using the daily divergence values, upwelling events are defined as continuous positive divergence and corresponds to uninterrupted equator ward wind parallel to the coast.

## **Appendix B**

### ***Temperature profiles***

See electronic files on accompanying CD for temperature profiles of the upper 100 and 200 m for each cruise.

## **Appendix C**

### ***Particle size spectra***

See electronic files on accompanying CD for individual figures of surface and chlorophyll maximum particle spectra constructed for each station sampled. Image files contain figures of normalized particle concentration against particle size for particles greater than  $4 \mu\text{m}$  and from the lower size limit sampled.

## **Appendix D**

### ***Expert system trail***

This appendix details the Expert system trail of the expert system created for this project in WinExp software. A trail is a printout of the context of the expert system and followed by the questions and rules of the expert system. 'D1' and 'D2' refer to the two decisions. 'Q1' to 'Q7' refer to the questions and 'A' refers to a possible answer. The "why" provides explanatory information to guide the user. 'IF' and 'THEN' statements explain the logic of the decisions and represent the rules. The expert system is available with the WinExp software in the electronic files on the accompanying CD.

Context: 'An expert system created to help the user determine what the dominant phytoplankton cell size they should expect to observe in particle spectra collected on

the St Helena Bay Monitoring Line (SHBML). Decisions take into account the position of the station, the state of upwelling and the dynamics of the upper water layer. Phytoplankton cell size is divided into small cells which are less than 10 microns equivalent spherical diameter (ESD) and intermediate to large cells which are greater than 10 microns ESD. The dominance of either small or large cells is based on size-based theory.

Created by Murray Crichton, as part of an MSc dissertation.

Details can be found in: Crichton, M. Are particle spectra in St Helena Bay an indication of the state of the phytoplankton community?, MSc dissertation, Marine Research Institute, Zoology Department, UCT. (in prep, Jan 2012).

Marine Research Institute, University of Cape Town, South Africa.'

D1: 'Small cells are likely to dominate surface waters'

D2: 'Intermediate to large cells are likely to dominate surface waters'

Q1: 'Where is the station in relation to the upwelling front?'

Why 'The upwelling front is the interface between offshore oceanic waters and inshore coastal waters. Beyond the upwelling front, surface waters originate from the Agulhas Bank and are generally warm and nutrient-poor.'

A1 'Landward of or in the front'

A2 'Offshore of the front'

Q2: 'Is the station in the inner bay (stations 1 to 3) or in the frontal area (stations 4 onwards)?'

Why 'The inner bay receives cold nutrient rich water from cyclonic circulation that originates from an upwelling centre off Cape Columbine, as well as from intermittent coastal upwelling in a narrow band north of St. Helena Bay when southerly alongshore winds prevail whereas stations in the frontal area are within the upwelling plume.'

A1 'Inner Bay'

A2 'Frontal Area'

Q3: 'Was upwelling active for three days prior to sampling?'

Why 'Active upwelling during sampling enriches the water with nutrients. The time frame of upwelling will influence whether large cells have enough time to grow to dominance.'

A1 'Yes'

A2 'No'

Q4: 'Was there sustained upwelling in the 20 days prior to sampling?'

Why 'Upwelling provides nutrient-rich water to the surface. Upwelling events over five to 15 days are important for phytoplankton growth.'

A1 'Yes'

A2 'No'

Q5: 'Were the surface waters well-mixed or stratified at the station?'

Why 'Well-mixed water indicates upwelling. As water ages at the surface it becomes warm and stratified. Warm stratified water is often nutrient-depleted. Stratification also indicates decreased turbulence'

A1 'Well-mixed'

A2 'Stratified'

Q6: 'Was there upwelling within three days prior to sampling?'

Why 'Upwelled water is readily depleted of nutrients at the surface. Within three days it is likely that nutrients will have already been depleted from the surface'

A1 'Yes'

A2 'No'

Q7: 'Was there upwelling within three days prior to sampling and within four to 11 days prior to sampling?'

Why 'Large slow-growing cells take longer to respond to a fresh injection of nutrients than rapidly dividing small cells.'

A1 'Only within 3 days'

A2 'Within 3 days and within 4-11 days'

Rule1

Why 'Offshore, and beyond the influence of coastal upwelling, nutrient-poor oceanic water from the Agulhas Bank favours the growth of small cells. In the dissertation data set this has been observed 15 out of 15 possible times (100% success rate).'

IF q1a2 THEN D1

Rule2

Why 'Quiescent upwelling conditions have prevailed for at least 20 days prior to upwelling and there has been no nutrient enrichment to the surface. Surface waters are likely to be nutrient-poor and therefore the growth of small cells is favoured. In the dissertation data set this has been observed 1 out of 1 possible times (100% success rate).'

IF q1a1 AND q2a1 AND q3a2 AND q4a2 THEN D1

Rule3

Why 'Nutrient-rich water from upwelling events off Cape Columbine within the past 20 days has recirculated in to the inner bay and provided sufficient nutrients for large cells to dominate surface waters. The surface waters have not stratified of yet indicating that

nutrients have not yet been removed from the water. In the dissertation data set this has been observed 4 out of 4 possible times (100% success rate).'

IF q1a1 AND q2a1 AND q3a2 AND q4a1 AND q5a1 THEN D2

#### Rule4

Why 'Nutrient-rich water from upwelling events off Cape Columbine within the past 20 days has recirculated in to the inner bay. However stratification of the water column by solar insolation indicates that the surface water is nutrient-depleted. Nutrient-poor waters favour the growth of small cells. In the dissertation data set this has been observed 3 out of 3 possible times (100% success rate).'

IF q1a1 AND q2a1 AND q3a2 AND q4a1 AND q5a2 THEN D1

#### Rule5

Why 'Active injection of nutrient-rich upwelled water within the inner bay favours the growth and dominance of larger cells. Even though waters may be warmed at the surface and stratification of the upper layer is occurring the sustained nutrient influx and seeding of large-celled phytoplankton upward results in large cells dominating the surface waters. In the dissertation data set this has been observed 1 out of 6 possible times (17% success rate).'

IF q1a1 AND q2a1 AND q3a1 THEN D2

#### Rule6

Why 'Upwelling has not occurred within three days prior to sampling. It is likely that surface waters have already been depleted of nutrients. Nutrient-poor water favours the growth of small cells. In the dissertation data set this has been observed 1 out of 1 possible times (100% success rate).

IF q1a1 AND q2a2 AND q6a2 THEN D1

#### Rule7

Why 'Upwelling has occurred within three days prior to sampling and injected nutrients, however, small rapidly-dividing cells take advantage of the conditions and large likely to dominate. Slower-growing larger cells have had insufficient time to grow and dominate surface waters. In the dissertation data set this has been observed 1 out of 1 possible times (100% success rate).'

IF q1a1 AND q2a2 AND q6a1 AND q7a1 THEN D1

#### Rule8

Why 'Upwelling has occurred within four to 11 days prior to sampling. Active injection of nutrients favours the growth of large cells. The time frame allows the slower growing

large cells to divide and dominate surface waters. In the dissertation data set this has been observed 1 out of 1 possible times (100% success rate).'

IF q1a1 AND q2a2 AND q6a1 AND q7a1 AND q5a1 THEN D2

#### Rule9

Why 'Upwelling has occurred within four to 11 days prior to sampling. However, water is highly stratified and most likely nutrient-depleted, probably because upwelling prior to sampling was weak. Small cells are likely to dominate surface waters because insufficient nutrients exist for large cells to dominate. In the dissertation data set this has been observed 6 out of 10 possible times (60% success rate).'

IF q1a1 AND q2a2 AND q6a1 AND q7a1 AND q5a2 THEN D1

University of Cape Town